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Vol. 79, No. 3 **July 1981**

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Seattle, Washington

U.S. DEPARTMENT OF COMMERCE

Malcolm Baldrige, *Secretary*

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NATIONAL MARINE FISHERIES SERVICE

Fishery Bulletin

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Seattle, Washington

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THE OSTEOLOGY AND RELATIONSHIPS OF THE ANGLERFISH GENUS *TETRABRACHIUM* WITH COMMENTS ON LOPHIIFORM CLASSIFICATION[1]

THEODORE W. PIETSCH[2]

ABSTRACT

The shallow-water anglerfish, *Tetrabrachium ocellatum*, now represented by 36 specimens from Australian, New Guinean, and Indonesian waters, is redescribed and compared osteologically with its allies within the Antennarioidei. Phylogenetic analysis based on a search for shared, derived characters shows that *Tetrabrachium* is most closely related to *Antennarius*, and is classified on this basis as a sister-family of the Antennariidae. That the Tetrabrachiidae has entered a "new adaptive zone" relative to the Antennariidae is evidenced morphologically by a number of unique derived features. The most conspicuous of these include small, close-set eyes protruding from the dorsal surface of the head, and a peculiar webbing between the pectoral fin and the body, and between the pectoral and pelvic fins, characters that reflect a benthic existence in soft substrata (mud or fine sand).

It is further shown that a group including the Antennariidae and Tetrabrachiidae forms the primitive sister group of the Lophichthyidae and that these two groups together form the primitive sister group of the Brachionichthyidae. Although evidence is provided to establish a sister-group relationship between the Chaunacidae and Ogcocephalidae, no convincing synapomorphy is known at the present time that will establish monophyly for a group containing all six families. An analytical key to the major subgroups of the Antennarioidei is provided and a revised classification of the order Lophiiformes is proposed.

One of the more curious forms described by Günther (1880) in his report on the shore fishes procured by the *Challenger* Expedition of 1873-76, was a single specimen of an antennarioid anglerfish from off the southern coast of New Guinea. In reference to a peculiar, double pectoral fin and numerous ocellilike markings on the dorsal half of the body, the species was named *Tetrabrachium ocellatum*. Since the original description perhaps a dozen authors have cited Günther (1880), but none have been able to offer any new information on this species other than a report of the discovery of two additional specimens (Whitley 1935). For the purposes of this study, 36 specimens of *T. ocellatum* have been located, all collected from Australian, New Guinean, and Indonesian waters at depths of between approximately 5 and 55 m. Although a close phylogenetic relationship with the genus *Antennarius* has been implied (by recognition of a subfamily Tetrabrachiinae of the Antennariidae; Regan 1912, Berg 1940, Norman 1966), no evidence for this alignment has been provided.

The objectives of this paper are to describe the structure of *T. ocellatum*, to compare it morphologically with its nearest allies, and to speculate on the phylogenetic relationships of this and other members of the suborder Antennarioidei. Representatives of the six major antennarioid subgroups (here recognized as families) are considered in detail. In addition to *Tetrabrachium*, these are *Antennarius* Daudin, recognized here as the least derived genus (see Phylogenetic Relationships below) of some eight genera of the Antennariidae (a modification of Schultz 1957; Pietsch in prep.); *Lophichthys*, a monotypic genus recently described by Boeseman (1964) and heretofore not adequately placed within any higher taxonomic category (see Boeseman 1964 and Le Danois 1979); *Brachionichthys* Bleeker (= *Sympterichthys* Gill), containing approximately four southern Australian species, and recognized as constituting an antennarioid family by nearly all authors since Regan (1912); *Chaunax* Lowe, the only genus of the family Chaunacidae; and *Dibranchus* Peters, an underived genus of the Ogcocephalidae (see Bradbury 1967).

[1]Contribution No. 561, College of Fisheries, University of Washington, Seattle, Wash.

[2]College of Fisheries, University of Washington, Seattle, WA 98195.

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METHODS AND MATERIALS

Standard lengths (SL) are used throughout. All measurements were taken on the left side and rounded to the nearest 0.5 mm. Head length is the distance from the anterior tip of the upper jaw to the posteriormost margin of the preopercle. The illicial bone is the first spinous dorsal ray (Bradbury 1967). Sockets indicating missing teeth in the jaws and on the vomer were included in total tooth counts. The analysis of relationships follows, in a general way, the phylogenetic approach suggested by Hennig (1966) with the exception that not all branching points in the cladogram are formally named. The loss of convenience in discussing individual sister groups by a single epithet is outweighed by the avoidance of adding a multiplicity of new taxonomic categories and names, as well as the necessity of altering names that are well established in the scientific literature. The relative primitiveness of character states is identified by the procedure of outgroup comparison as discussed by Eldredge and Cracraft (1980:63).

The osteology of *Tetrabrachium ocellatum* is based on two specimens (AMS IB.7177, 7178, 56 and 61 mm SL) cleared and stained with alizarin red S following the trypsin digestion technique of Taylor (1967). All additional material examined for comparative purposes is listed in the Appendix. Bone terminology follows Nybelin (1963), Bradbury (1967), and Pietsch (1972). In osteological drawings cartilage is stippled, and where necessary for clarity, open spaces are rendered in solid black.

Material is deposited in the following institutions:

AMS: Australian Museum, Sydney
BMNH: British Museum (Natural History), London
KFRS: Kanudi Fisheries Research Station, Konedobu, Papua, New Guinea
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge
NMV: National Museum of Victoria, Melbourne
RMNH: Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands
USNM: National Museum of Natural History, Washington, D.C.
UW: College of Fisheries, University of Washington, Seattle
WAM: Western Australian Museum, Perth

SYSTEMATICS

Tetrabrachium ocellatum Günther
Figures 1, 2

Tetrabrachium ocellatum Günther 1880:44-45, 78, pl. 19, fig. C (original description, single specimen, 51 mm SL, holotype BMNH 1879.5.14.618, *Challenger* Station 188, south of New Guinea, 9°59′ S, 139°42′ E, 51 m). Gill 1883:551 (after Günther 1880; Pedicalidae of Günther 1880:78 a misprint for Pediculati). Regan 1912:283 (after Günther 1880; Tetrabrachiinae). Fowler 1928:476 (after Günther 1880; Pedicalidae after Günther 1880:78). Gregory 1933:394 (after Günther 1880). Whitley 1934:xxx (second known specimen). Whitley 1935:249 (second and third known specimens; Tetrabrachiidae). Berg 1940:499 (subfamily Tetrabrachiini of Antennariidae). Gregory 1951:224, fig. 9.154C (obliteration of postopercular cleft by branchiostegal membrane). Beaufort and Briggs 1962:222, fig. 50 (description, holotype reexamined). Le Danois 1964:141 (after Günther 1880, Whitley 1935). Norman 1966:590 (in key; Tetrabrachiinae of Antennariidae). Kailola and Wilson 1978:26, 58-59 (additional material, Papua New Guinea).

Material.—Thirty-six specimens, 17-67 mm SL.

Holotype of *T. ocellatum*: BMNH 1879.5.14.618, 51 mm SL, *Challenger* Station 188, south of New Guinea, 9°59′ S, 139°42′ E, 51 m.

Additional nontype material: AMS IB.5836, 64 mm SL, Townsville District, Queensland, 19°16′ S, 146°49′ E, trawled. AMS IA.6003, 17 mm SL, off Hayman Island, Queensland, 20°03′ S, 148°53′ E, 9 m. AMS IA.6136, 27 mm SL, Lindeman Island, Queensland, 1934. AMS IA.6759, 2(20 and 26.5 mm SL), Lindeman Island, Queensland, 20°27′ S, 149°02′ E, trawled. AMS IB.7173-7178, 6(42.5-61 mm SL), Gulf of Carpentaria, Queensland (56 and 61 mm SL specimens cleared and stained). AMS I.15557-281, 7(42-61.5 mm SL), Gulf of Carpentaria, Queensland, 17°29′ S, 140°24′ E, trawled, 5.5 m, 24 November 1963. AMS I.19289-003, 31.5 mm SL, *Alpha Helix*, Arafura Sea, 10°27.5′ S, 136°47.0′ E, trawled on bottom of mud, gravel, and shells, 55 m, 17 March 1975. AMS I.20907-041, 41.5 mm, south of Cooktown, Queensland, 16°01′ S, 145°29′ E, trawled on bottom of mud and shells, 20 m, 6 February 1979.

KFRS 871, 46 mm SL, northwest of Yule Island, Gulf of Papua, New Guinea, March 1963. KFRS 1483, 52 mm SL, Kerema Bay, Gulf of Papua, 5 May 1969. KFRS 2953, 62 mm SL, 6.5-8 km off Kerema Point, Gulf of Papua, prawn trawl, 14.6 m, 9 May 1973. KFRS 3017, 58 mm SL, Kerema Bay, Gulf of Papua, 9-13 m, September-October 1970. KFRS 3023, 61 mm SL, Kerema Bay, Gulf of Papua, 9-13 m, September-October 1970. KFRS 3082, 50 mm SL, FRV *Rossel*, Yule Island, Gulf of Papua, trawl, 18-24 m, January-February 1971.

USNM 177873, 52 mm SL, between Hayman and Magnetic Islands, Queensland, trawl, 18-46 m, May-June 1957.

WAM P.21473-001, 67 mm SL, Vansittart Bay, West Australia, 14°04′ S, 126°17′ E, 26 May 1968. WAM P.26130-001, 2(58 and 67 mm SL), Broome Bay, Napier, West Australia, 14°00′ S, 126°36′ E, 26 November 1968. WAM P.26832-001, 34 mm SL, Wokam and Uru Islands, Indonesia, 5°30′ S, 134°12′ E, 15 June 1970. WAM P.26833-001, 47 mm SL, Aru Island, Indonesia, 5°30′ S, 134°12′ E, 16 June 1971. WAM P.26540-001, 53 mm SL, Mermaid Passage, Dampier Arch, West Australia, 16°25′ S, 123°20′ E, prawn trawl, 8 September 1977. WAM P.26834-001, 35 mm SL, west of Dongara, West Australia, 29°15′ S, 114°01′ E, 20 March 1972.

Diagnosis.—Mouth small, opening dorsally, bones of jaws nearly vertical, nearly completely hidden by folds of skin; lower lip lined with small, cutaneous papillae; eyes small, close-set, protruding from dorsal surface of head; anterior half of frontals separate, posterior half meeting on midline; pterosphenoid present; parietals separated by supraoccipital; mesopterygoid absent; ectopterygoid triradiate, T-shaped; dorsal head of quadrate narrow, less than width of metapterygoid; interhyal with a medial, posterolaterally directed process; interopercle flat, broad; pharyngobranchial I present; epibranchial teeth absent; ceratobranchials toothless; toothed portion of ceratobranchial V expanded; hypohyals II and III bifurcated; ossified basibranchials absent; small basihyal present; neural spines of preural centra 14-22 short, spatulate, not interdigitating with proximal radials of soft dorsal fin; epurals absent; three dorsal fin spines without interconnecting membrane; illicial cavity absent (Bradbury 1967); illicium reduced, without esca, emerging anterior to eyes; second dorsal fin spine covered with cutaneous filaments, emerging from between eyes; third dorsal fin spine nearly completely covered with skin of head, distal tip emerging on posterior margin of cranium; illicial pterygiophore and pterygiophore of third dorsal fin spine with highly compressed, bladelike dorsal expansions, each expansion with a foramen within which lie medially directed prongs of proximal end of respective dorsal fin spine; soft dorsal fin rays 16-17; anal fin rays 11-12; pectoral fin rays 9, divided into dorsal portion of 4 rays interconnected by membrane, ventral portion of 5 interconnected rays, dorsalmost ray attached to lateral surface of body by membrane; pectoral lobe attached to posteriormost ray of pelvic fin by membrane; three pectoral radials; skin naked except for very few microscopic spinules associated with pores of acoustico-lateralis system.

Description (Figure 1).—Body strongly compressed, elongate (greatest depth <50% SL); head compressed, short (<32% SL); cranium strongly oblique in position, posterior end of cranium and anterior vertebrae raised forming a prominent convex hump; mouth small, width <16% SL;

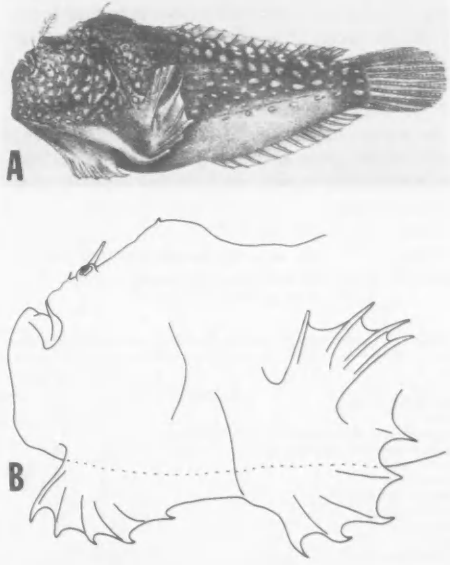

FIGURE 1.—*Tetrabrachium ocellatum*: A. Holotype, BMNH 1879.5.14.618, 51 mm SL, after Günther 1880; B. Diagram showing webbing between lower portion of pectoral fin and body, and between pectoral and pelvic fins.

anterior nostril opening on edge of upper lip, posterior nostril opening approximately half-way between edge of lip and eye; oral valve present lining both upper and lower jaw; gill opening small, situated just below and behind base of pectoral fin lobe; no opening behind fourth gill arch; holobranchs present on ventral half of ceratobranchial I, full length of ceratobranchials II and III, ventral half of epibranchial II, and ventral tip of epibranchial III; hemibranchs present on dorsal half of ceratobranchial IV and ventral tip of epibranchial IV; pseudobranch absent; swim bladder absent; ovaries paired.

Pterygiophore of illicium completely covered with skin of head; illicial bone short (<8% SL) and thin, tapering to a point; bases of soft dorsal and anal fins long (>48% and 42% SL, respectively), rays short; dorsal and anal fin rays enveloped in membrane; in some specimens (7 of 16 specimens examined) distal tips of first 9 rays of soft dorsal fin free, each terminating in a tight ball of tissue, remaining dorsal rays enveloped in membrane; caudal fin long (>30% SL), rounded.

Teeth small, slender, recurved, and depressible; each premaxilla with a single row of 22-25 teeth, each dentary with approximately 35 teeth arranged in two rows; vomerine teeth in two patches, about 25 teeth in each patch; palatine teeth absent; pharyngobranchials II and III and ceratobranchial V toothed.

Color in preservative white on lower half of body to brown on upper half of body, with numerous, small, white spots continuing onto soft dorsal fin, remaining fins white; oral cavity and viscera unpigmented.

Length to 67 mm SL.

Complete counts and measurements of representative material are given in Table 1.

Habitat.—Specific information on the habitat frequented by *T. ocellatum* is available for only two captures: a 31.5 mm SL specimen (AMS I.19289.003) and a 41.5 mm SL specimen (AMS I.20907-041) were trawled off a bottom of mud, gravel, and shell. A number of other specimens were collected in prawn trawls most likely fished over similar, soft-bottom substrates of mud or sand.

Distribution (Figure 2).—*Tetrabrachium ocellatum* is known from 36 specimens collected in shallow water (55 m or less) off the western (as far south as lat. 29° S) and northern coasts of Australia, the southern coast of Papua, New Guinea, and the south Molucca Islands, Indonesia.

Osteology of *Tetrabrachium ocellatum*
Figures 3-13

The osteology of lophiiform fishes has been dealt with by numerous authors (Garman 1899; Regan

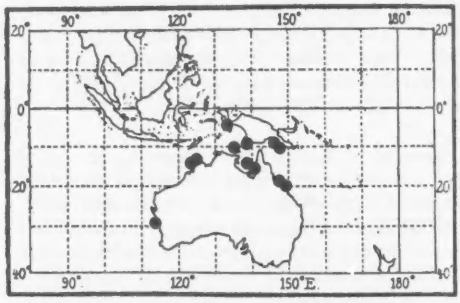

FIGURE 2.—Known distribution of *Tetrabrachium ocellatum*. One symbol may indicate more than one capture.

TABLE 1.—Counts and measurements (in percentage of standard length) of representative specimens of *Tetrabrachium ocellatum*.

	KFRS 3087	UW 20771	AMS IB.7173	KFRS 871	KFRS 3082	USNM 177873	AMS IB.7174	AMS IB.7175	KFRS 3023	KFRS 2953
Standard length, mm	39	39.5	42.5	46	50	50.5	54	56	61	62
Length:										
Head (snout to posteriormost margin of preopercle)	27.7	30.4	25.9	26.1	26.0	23.8	20.4	25.0	23.0	22.6
Snout to emergence of dorsal spine III	22.6	25.3	25.9	25.4	23.2	23.8	25.0	—	23.0	25.0
Illicial bone	7.2	4.6	2.6	4.1	4.0	4.0	3.3	—	—	4.8
Dorsal spine II	7.9	6.3	4.7	8.7	6.8	5.2	4.1	4.6	5.4	4.8
Base of soft dorsal fin	67.9	64.6	49.4	56.5	58.0	63.4	63.0	—	54.9	53.2
Base of anal fin	51.3	51.9	42.3	48.9	51.0	53.5	49.1	—	48.4	48.4
Caudal fin	43.1	36.2	39.3	34.8	32.0	35.6	36.1	36.7	37.7	33.9
Width:										
Between eyes (from center of lens)	11.0	12.4	10.6	11.1	10.4	9.9	9.1	—	10.8	10.3
Least between frontal bones	6.7	6.8	4.9	6.1	5.8	5.5	5.4	—	4.9	5.6
Greatest between sphenotic bones	20.2	19.7	19.8	20.6	19.4	19.2	17.2	17.9	20.5	20.2
Greatest body depth	38.5	43.0	35.3	46.7	46.0	45.5	42.6	37.5	42.6	41.9
Dorsal fin rays	16	17	16	16	16	17	16	16	17	16
Anal fin rays	11	11	11	11	11	12	12	11	12	12

1903, 1912; Gregory 1933; Eaton et al. 1954; Monod 1960; Le Danois 1964, 1974, 1979; Field 1966; Bradbury 1967; Rosen and Patterson 1969; and additional references cited by Pietsch 1972, 1974, 1978, 1979), yet no published osteological information on the genus *Tetrabrachium* is available. In the following account only those comparative aspects that differ from those previously described in other anglerfishes are discussed.

Cranium (Figures 3-6).—The ethmoid cartilage of *T. ocellatum* broadly covers the posterior half of the vomer meeting with the lateral ethmoids laterally and the supraethmoid medially. The supraethmoid forms a narrow, vertical interorbital septum lying between, but well separated from the orbital portions of the frontals. The laterally compressed, ventral end of the supraethmoid meets with the ethmoid cartilage anteriorly and lies within a groove on the dorsal surface of the parasphenoid posteriorly. The dorsal end of the supraethmoid is overlapped on each side by central extensions of the frontals. Each lateral ethmoid has a narrow, cylindrical posterior portion that lies ventral to an anterior extension of the respective frontal, and a larger, ventrally directed, anterior portion that meets with the ethmoid cartilage.

The head of the vomer lies ventral to the ethmoid cartilage. Its anterior margin is indented medially. The ventral surface of the vomer is strongly concave (as seen in anterior view, Figure 6). A laterally compressed, keellike posteromedial process emerges from the ventral surface of this bone and fits within a deep groove on the anteroventral surface of the parasphenoid; the ventral margins of the posteromedial process of the vomer and the anterior end of the parasphenoid are strongly convex (as seen in lateral view, Figure 4). Vomerine teeth are present in two lateral patches, each patch containing approximately 25 teeth arranged in perhaps three irregular rows.

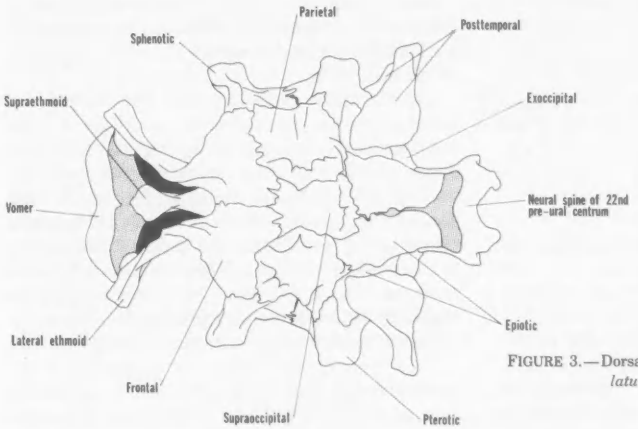

FIGURE 3.—Dorsal view of cranium of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL.

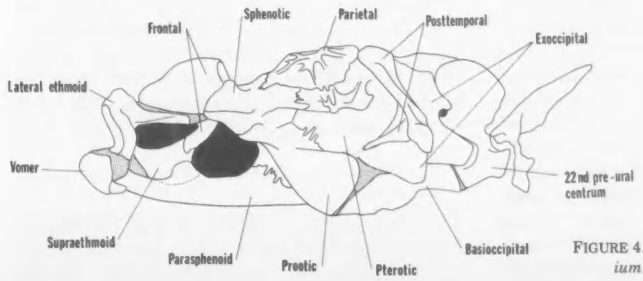

FIGURE 4.—Lateral view of cranium of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL.

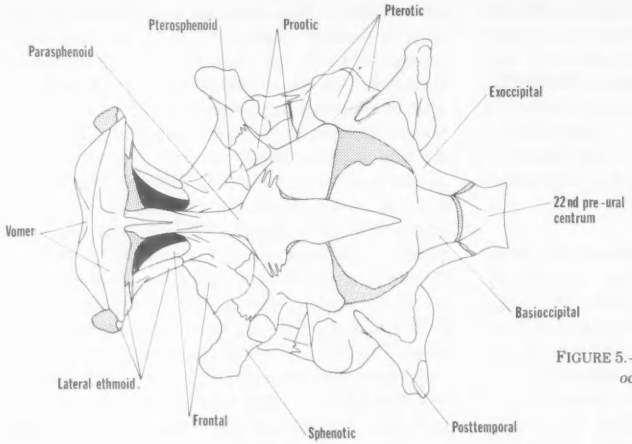

FIGURE 5.—Ventral view of cranium of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL.

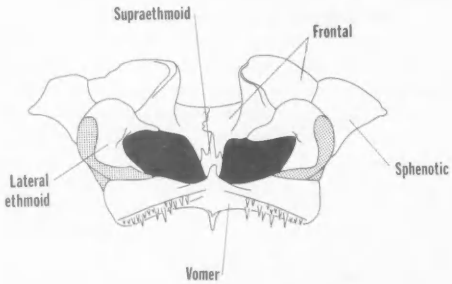

FIGURE 6.—Anterior view of cranium of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL.

The frontals are relatively large and irregular in shape. Each has a laterally compressed, anterior half, well separated from its counterpart of the other side, and a dorsoventrally depressed posterior half that meets its counterpart on the midline. In dorsal view (Figure 3), the frontals form a relatively narrow orbital region to accommodate the closely set, dorsally directed eyes. In lateral view (Figure 4), the depressed posterior half of the frontals form a concavity between the elevated, laterally compressed anterior half of these bones and the posterior half of the cranium.

The parietals are irregularly shaped elements with deeply pitted and grooved external surfaces. They are well separated from each other by the supraoccipital. Each parietal overlaps the respective frontal anteriorly, the sphenotic and pterotic laterally, the supraoccipital medially, and the epiotic posteriorly.

A small pterosphenoid lies on the ventromedial surface of the frontal in contact with the prootic.

The orbitosphenoid and basisphenoid are absent in all lophiiforms.

The parasphenoid is a stout, well-ossified element with a convex ventral margin (Figure 4). Its anterior end is overlapped by the ethmoid cartilage dorsally and by the narrow shaft of the vomer ventrally. Medially, the dorsal surface of this bone forms a deep groove within which lies the laterally compressed, posteroventral part of the supraethmoid. Posteriorly, the parasphenoid is broadly connected with the prootics laterally and the basioccipital medially. At no point does the parasphenoid make contact with the frontals.

Each sphenotic forms a dorsoventrally depressed flange that extends outward in an anterolateral direction, considerably beyond the width of the ethmovomerine region of the cranium (Figure 3).

The remaining elements of the cranium (pterotics, epiotics, prootics, supraoccipital, and exoccipitals) do not differ substantially from those described for other lophiiforms (Regan 1912, fig. 5; Gregory 1933, fig. 265, 267-271; Pietsch 1972, 1974).

Otoliths (Figure 7).—The sagitta of *T. ocellatum* is roughly oval in shape with a length to height ratio of about 1.4:1. The sulcus is only slightly

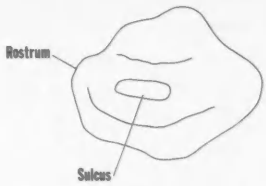

FIGURE 7.—Medial view of right sagitta of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL.

grooved. The rostrum is poorly developed, and an antirostrum is absent.

Mandibular arch (Figures 8, 9).—The premaxillae (Figure 8) are each characterized by having a narrow ascending process, nearly as long as the tapering toothed portion of the bone; a rounded articular process; and an elongate, spatulate postmaxillary process (pmpmx of Rosen and Patterson 1969, fig. 56A). The ascending and articular processes together form an oblique angle with the postmaxillary and toothed processes. The toothed portion of each premaxilla bears a single row of 22 to 25 depressible teeth, the largest at the symphysis, becoming progressively smaller posteriorly.

Each maxilla consists of a broad posterior portion (completely hidden from behind by a thick fold of skin when the mouth is closed), and an expanded anterior head that, in turn, consists of an anterior process that overlaps the respective premaxilla and a medially directed process that is attached by a short ligament to the articular process of the respective premaxilla. The dentaries, articulars, and angulars (Figure 9) are

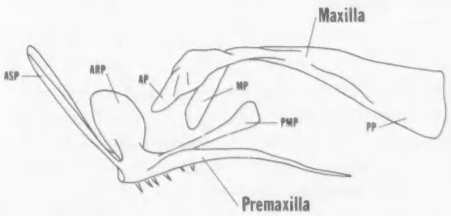

FIGURE 8.—Upper jaw bones of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL. AP = anterior process of maxilla; ARP = articular process of premaxilla; ASP = ascending process of premaxilla; MP = medial process of maxilla; PMP = postmaxillary process of premaxilla; PP = posterior process of maxilla.

similar to those described for other lophiiforms (Gregory 1933, fig. 265, 266, 269-271; Pietsch 1972, 1974). Each dentary bears approximately 35 depressible teeth arranged in two rows.

Palatine arch (Figure 9).—Each metapterygoid is in contact with four other bones: dorsally and posterodorsally with the hyomandibular, posteroventrally with the upper half of the symplectic, and ventrally with the quadrate and ectopterygoid. The ectopterygoid is large and T-shaped, overlapping the medial surface of the metapterygoid dorsally, the quadrate ventrally, and the palatine anteriorly. The mesopterygoid (cartilaginous or ossified) is absent. The palatine is unusually large, approximately twice the length of the ectopterygoid. Palatine teeth are absent.

Hyoid arch (Figures 9, 10).—Dorsally, each hyomandibular is forked forming two heads, both of which articulate with the cranium: an anterior head fits into a concavity formed by the sphenotic and prootic, and a posterior head articulates on the ventrolateral face of the pterotic (Figures 4, 5, 9). The symplectic is separated from the hyomandibular by cartilage dorsally, and lies within a shallow groove on the medial surface of the quadrate ventrally. The dorsal head of the quadrate is narrow, considerably less than the width of the metapterygoid. The interhyal bears a prominent medial, posterolaterally directed process that wraps around the posterior margin of the respective preopercle when the interhyal rotates upward (e.g., during a feeding event). This contact between the interhyal and the preopercle limits the dorsal rotation of the interhyal and, in turn, limits the extent of abduction of the lower jaw via ligamentous connections to the respective interopercle.

The epihyal and ceratohyal do not differ substantially from those described for other lophiiforms (Pietsch 1974, 1979). There are two hypohyals on each side (Figure 10), both of which are connected to the ceratohyal by a posteriorly directed strut. The dorsal hypohyal is further connected to an anterodorsal extension of the ceratohyal by a cylindrical piece of cartilage.

There are six branchiostegal rays all borne on the ceratohyal (Figure 10); the two anteriormost rays articulate on the medial surface, the four posterior rays on the lateral surface. Branchiostegal rays 3 and 4 are curved in an anteroventral direction, in contrast to the posterodorsal direc-

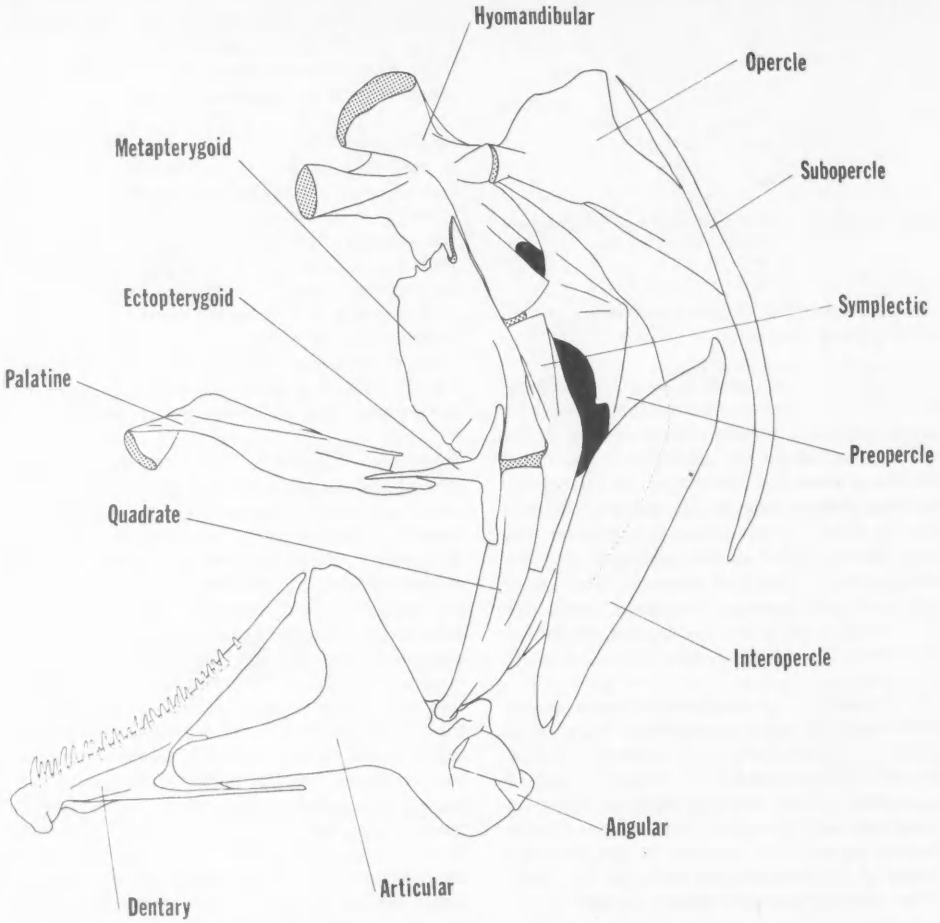

FIGURE 9.—Medial view of lower jaw, suspensorium, interhyal, and opercular apparatus of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL, right side.

tion of the remaining rays. On the left ceratohyal of the 61 mm cleared and stained specimen of *T. ocellatum* (Figure 10), the fifth branchiostegal ray is bifurcated at midlength, giving the impression of having seven total rays.

A small, triangular basihyal is present (Figure 10). The urohyal is absent in all lophiiforms.

Opercular apparatus (Figure 9).—The opercle is triangular in shape with a slightly concave posterior margin. An elongate, crescent-shaped subopercle lies medial to the ventral tip of the opercle. A subopercular spine is absent. The interopercle is large, flat, and broad. The crescent-shaped preopercle is also large, strengthening the entire length of the suspensorium.

Branchial arches (Figure 11).—There are three pharyngobranchials. That of the first arch is a small, toothless, suspensory pharyngobranchial; those of the second and third arches are considerably larger, tooth-bearing elements closely at-

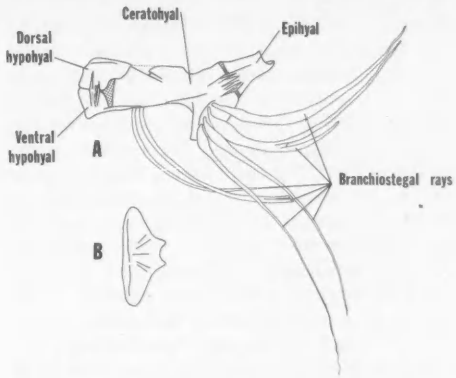

FIGURE 10.—Hyoid apparatus of *Tetrabrachium ocellatum*: A. AMS IB.7178, 61 mm SL, left lateral view; B. Basihyal, AMS IB.7177, 56 mm SL, ventral view, anterior to the left.

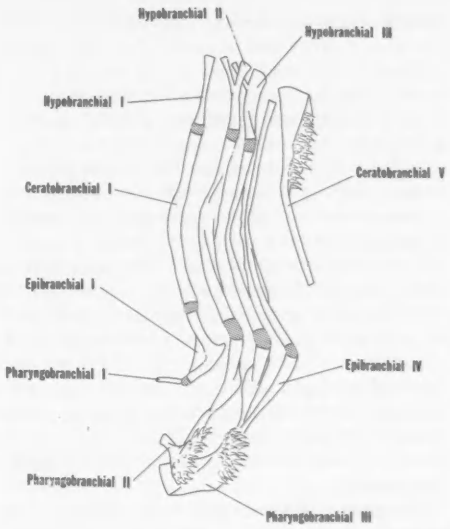

FIGURE 11.—Branchial arches of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL. The ventral portion of the branchial basket is shown in dorsal view; the dorsal portion (epibranchials and pharyngobranchials) is folded back and shown in ventral view.

tached to each other and to the dorsal end of epibranchials II through IV. Epibranchial I is triradiate in shape, articulating with ceratobranchial I proximally, bearing pharyngobranchial I distally, and attached by a short ligament to the proximal end of epibranchial II medially. Ceratobranchials I through IV are toothless. The expanded, proximal end of each ceratobranchial V bears about 19 to 21 depressible teeth arranged in two rows. Hypobranchial I is a simple, rod-shaped element. Hypobranchials II and III are bifurcated proximally. Ossified basibranchials are absent.

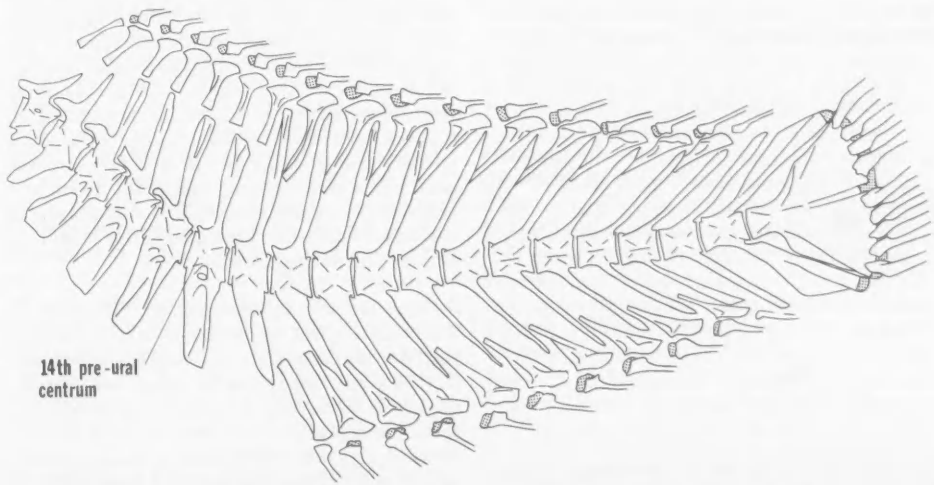

FIGURE 12.—Vertebrae, caudal skeleton, and median fins of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL.

Vertebrae and caudal skeleton (Figure 12).—In the two cleared and stained specimens of *T. ocellatum* examined, there are 22 vertebrae (including the last centrum to which is fused the hypural plate; Pietsch 1972:38). Preural centra 2 through 18 bear complete haemal arches and are considered caudal vertebrae. The neural spines of preural centra 14 through 22 are considerably shorter than those of the more posterior centra; correspondingly, the seven anteriormost proximal radials of the soft dorsal fin are also short so that they do not interdigitate with the respective neural spines. Further, there appears to be little if any connective tissue between the elements of the soft dorsal fin and the vertebral column in this region allowing for independent movement of the anterior portion of the fin relative to the axial skeleton. The haemal spines of preural centra 14 through 17 are unusually broad and laterally compressed.

The hypural plate, slightly notched posteriorly, bears the overlapping bases of nine principle caudal rays. The central seven caudal rays are bifurcated distally. There are no epurals.

Median fins and illicial apparatus (Figures 12, 13).—The spinous dorsal fin consists of three spines. The anteriormost two are supported by a single, elongate, horizontally situated pterygiophore (Figure 13) that is loosely attached to the dorsal surface of the cranium between the anterior halves of the frontal bones by three pairs of extrinsic illicial muscles (Bertelsen 1951:18, fig. 4; Bradbury 1967, fig. 2; Winterbottom 1974:284, fig. 44). The illicial bone (Bradbury 1967:401) is considerably reduced in size relative to other lophiiforms (Gregory 1933, fig. 265, 266, 267; Pietsch 1972, 1974, 1979). The second spine is considerably thicker and approximately three times longer than the first. The third spine, slightly longer and thicker than the second, is supported by a second, elongate, and horizontally placed, cephalic pterygiophore that is tightly connected to the posterior, dorsomedial surface of the supraoccipital and anterior, dorsomedial margins of the epiotics. The proximal end of each spine is bifurcated, each fork bearing a small, medially directed prong; the prongs of each spine fit within a large, rounded foramen located on a highly compressed, bladelike dorsal expansion of the respective pterygiophore.

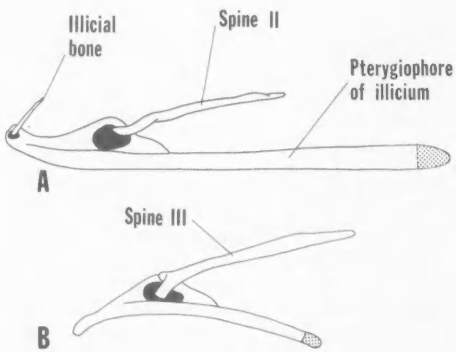

FIGURE 13.—Spinous dorsal fin of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL: A. Illicial apparatus, second dorsal spine, and common pterygiophore; B. Third dorsal spine and pterygiophore.

The soft dorsal fin consists of 16 biserial, segmented, and unbranched rays, each supported by a cartilaginous distal radial and an ossified proximal radial. The proximal end of the anteriormost proximal radial lies above the neural spine of the 19th preural centrum, while the proximal end of the last proximal radial lies between the neural spines of the fourth and fifth preural centra.

The anal fin consists of 11 biserial, segmented, and unbranched rays. The first two rays share a single supporting radial. The remaining rays are each supported by a small, cartilaginous distal radial and an elongate, ossified proximal radial. The proximal ends of the two anteriormost proximal radials lie between the haemal spines of the 12th and 13th preural centra. The proximal radials of the nine remaining anal fin rays have a one-to-one correspondence with the haemal spines, so that the radial of the last anal ray lies between the haemal spines of the fourth and fifth preural centra. The posteriormost rays of the dorsal and anal fins are broadly connected by a membrane to the dorsal and ventral margins of the caudal fin so that a caudal peduncle is absent.

Pectoral and pelvic girdles and fins (Figure 14).—The posttemporal is unusually large and connected to the posterolateral corner of the cranium in such a way as to allow for considerable movement (relative to the cranium) in an anterodorsal-posteroventral plane. The bone consists of a broad, dorsal flange that overlaps the dorsolateral surface of the epiotic, pterotic, and exoccipital. A large ligament originates on the posterodorsal margin of the prootic and inserts on the tip of

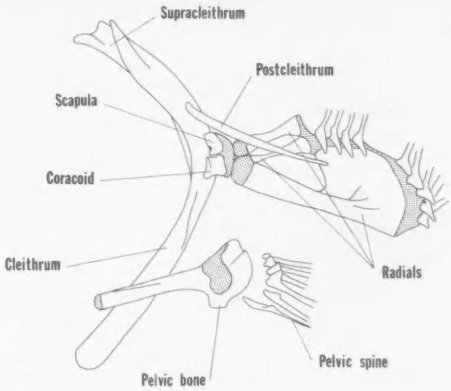

FIGURE 14.—Medial view of right pectoral girdle, and pectoral and pelvic fins of *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL. Cartilaginous radials supporting pelvic fin rays and cartilaginous distal radials supporting pectoral fin rays not shown; see text.

an elongate, ventromedially directed extension of the posttemporal.

The supracleithrum, cleithrum, coracoid, and scapula (Figure 14) are similar to those described for other lophiiforms (Gregory 1933, fig. 265; Pietsch 1972, 1974). A cleithral spine is absent. There is a single rodlike postcleithrum.

The pectoral fin is supported by three pectoral radials (Figure 14). The two dorsalmost radials are similar in size and shape. The third or ventralmost radial is considerably larger; its expanded distal portion bears the bases of nine unbranched, pectoral fin rays (each ray associated with a small, cartilaginous distal radial; not shown in Figure 14). The pectoral fin itself is divided into two portions: a dorsal portion consisting of four rays that are interconnected by a membrane, and a ventral portion consisting of five rays that are similarly connected to each other, but also to the lateral surface of the body. In a similar way, the pectoral fin lobe is connected by a membrane to the rays of the respective pelvic fin (Figure 1B). The pelvic bone, nearly as long as the ventralmost pectoral radial, bears on its expanded distal end a single spine and five unbranched pelvic fin rays (each ray associated with a small, cartilaginous radial; not shown in Figure 14).

Skin spines.—Dermal spines are absent except for the very rare occurrence of a tiny, crescent-shaped spinule associated with an individual pore of the acoustico-lateralis system of the head and trunk.

COMPARATIVE OSTEOLOGY OF ANTENNARIOID FAMILIES

The following discussion is based primarily on an osteological comparison of a representative of each of six major subgroups of the Antennarioidei (here recognized as families; see Phylogenetic Relationships and Appendix below): *Antennarius* Daudin, thought to be the least derived genus of the Antennariidae (see Phylogenetic Relationships below); *Tetrabrachium* Günther, the only genus of the Tetrabrachiidae; *Lophichthys* Boeseman, the only genus of the Lophichthyidae; *Brachionichthys* Bleeker, the only extant genus of the Brachionichthyidae (see p. 416); *Chaunax* Lowe, the only genus of the Chaunacidae; and *Dibranchus* Peters, an underived genus of the Ogcocephalidae (see Bradbury 1967). Only those comparative aspects that might have a bearing on the phylogenetic interrelationships of these taxa are discussed.

Cranium (Figures 3-6, 15-19).—In *Tetrabrachium* and *Antennarius* the ventral surface of the vomer is strongly concave (as seen in anterior view, Figure 6). A laterally compressed, keellike posteromedial process emerges from the ventral surface of this bone and fits within a deep groove on the anteroventral surface of the parasphenoid; the ventral margins of the posteromedial process of the vomer and the anterior end of the parasphenoid are strongly convex (as seen in lateral view, Figure 4). In all other antennarioids examined the posteromedial process of the vomer is flush with the more or less flat ventral surface of this bone; the ventral margins of the vomer and anterior end of the parasphenoid (as seen in lateral view) are straight to slightly concave.

Other osteological variation in the crania of antennarioids occurs primarily in the shape and relative position of the frontal bones. In *Antennarius*, *Lophichthys*, *Brachionichthys*, and *Dibranchus* (Figures 15-17, 19) the frontals are broad and roughly triangular in shape, well separated from each other anteriorly, but meeting on the midline posteriorly. The narrow interorbital space formed by these elements in *Tetrabrachium* is absent (compare Figures 3 and 15). The anterior ends of the frontals of *Lophichthys* are exceptionally narrow, gradually tapering to a point (Figure

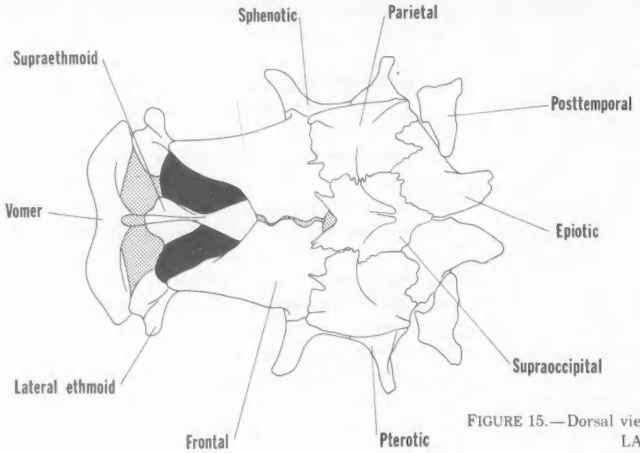

FIGURE 15.—Dorsal view of cranium of *Antennarius sanguineus*, LACM 8125, 76 mm SL.

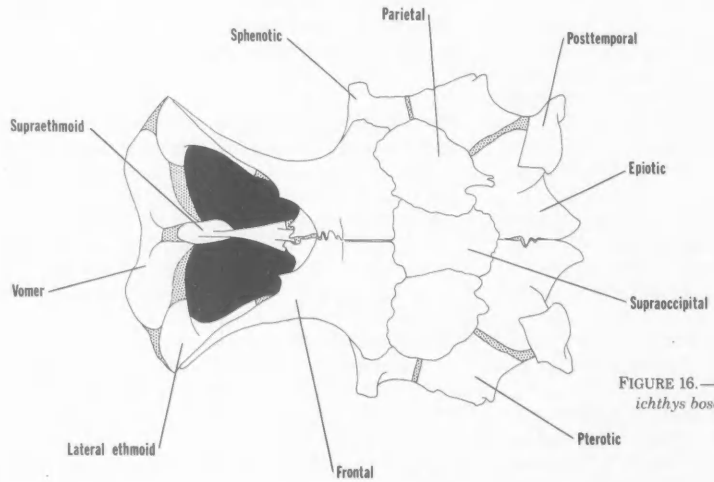

FIGURE 16.—Dorsal view of cranium of *Lophichthys boschimai*, UW 20773, 47 mm SL.

16); they diverge laterally to a much greater extent than in the other genera examined in response to a much wider vomer and laterally expanded lateral ethmoids.

In contrast to all other antennarioids examined, the frontals of *Chaunax* (Figure 18) are elongate and narrow, meeting on the midline for their entire length. The lateral ethmoids of this genus are also unusually long and narrow.

In *Antennarius*, *Lophichthys*, *Tetrabrachium*, *Chaunax*, and *Dibranchus* the parietals are well separated from each other by the supraoccipital. In *Brachionichthys*, however (Figure 17), these elements approach each other above the supraoccipital and meet on the midline, roofing over a small longitudinal passageway within which lies the posterior tip of the pterygiophore of the third dorsal fin spine.

Mandibular arch (Figures 8, 9, 20-25).—The premaxilla of *Antennarius* is very similar to that of *Tetrabrachium* (Figures 8, 20A); both genera

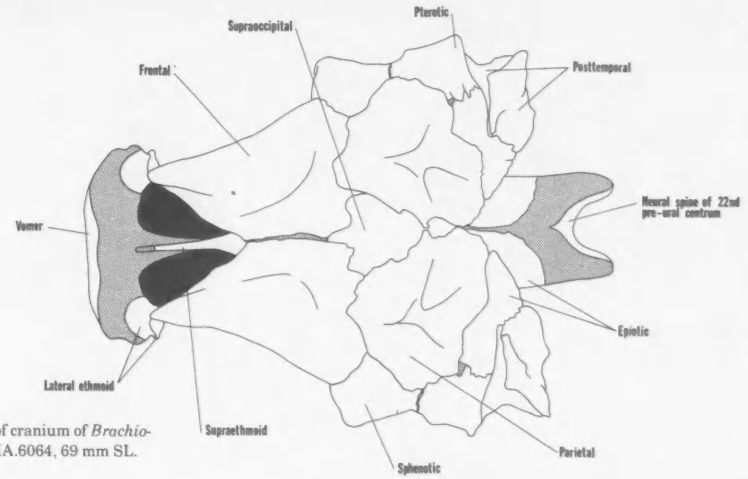

FIGURE 17.—Dorsal view of cranium of *Brachionichthys hirsutus*, AMS IA.6064, 69 mm SL.

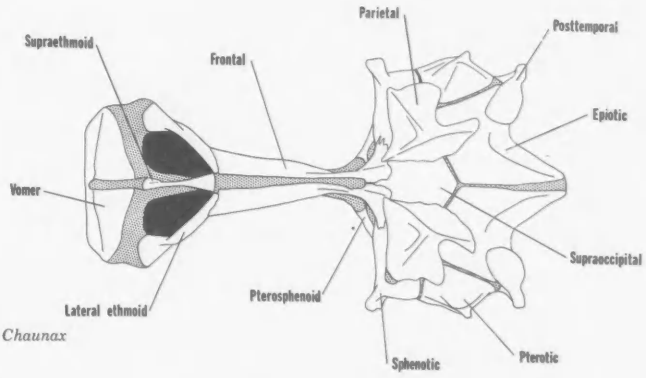

FIGURE 18.—Dorsal view of cranium of *Chaunax pictus*, UW 20770, 90 mm SL.

are characterized by having a spatulate postmaxillary process. The premaxilla of *Lophichthys* is also quite similar but bears a narrow, tapering postmaxillary process (Figure 20B). The premaxillae of the remaining antennarioid taxa examined are each somewhat different from these and from each other. In *Brachionichthys* (Figure 20C), the ascending and articular processes are at right angles to the toothed portion of the bone; the toothed portion is unusually short, about as long as the postmaxillary process and considerably shorter than the ascending process. In *Chaunax* (Figure 20D), the shape and relative proportions of the ascending, articular, and toothed processes of the premaxilla are similar to those of *Antennarius* and *Tetrabrachium*; the postmaxillary process, however, is represented by a large flange of bone, broadly connected to the toothed process. In *Dibranchus* (Figure 20E), the ascending and articular processes together form an acute angle with the postmaxillary and toothed processes; the articular process is nearly as long as the ascending process; and the postmaxillary process is connected by bone to the toothed process of the premaxilla for about half its length.

Palatine arch (Figures 9, 21-25).—A mesopterygoid is present in *Antennarius*, *Chaunax*, and

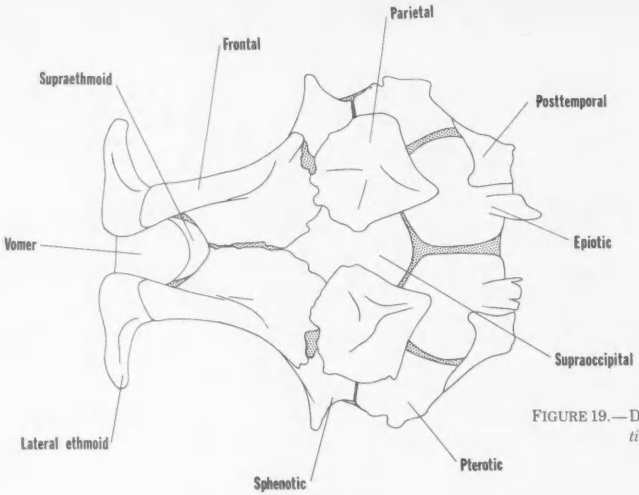

FIGURE 19.—Dorsal view of cranium of *Dibranchus atlanticus*, MCZ 51257, 105 mm SL.

Dibranchus (Figures 21, 24, 25), but absent in *Tetrabrachium*, *Lophichthys*, and *Brachionichthys* (Figures 9, 22, 23). The triradiate ectopterygoid of *Antennarius*, *Tetrabrachium*, and *Lophichthys* (T-shaped in *Tetrabrachium* and *Antennarius*, Figures 9, 21, but Y-shaped in *Lophichthys*, Figure 22) overlaps the medial surface of the metapterygoid dorsally; in *Chaunax* and *Dibranchus* the ectopterygoid is crescent-shaped and makes no contact with the metapterygoid. An ectopterygoid is absent in the larger (69 mm SL) specimen of *Brachionichthys* examined (Figure 23A) but represented by a small, weakly ossified remnant in the smaller specimen (42 mm SL) (Figure 23B).

The palatine is well toothed in *Antennarius*, *Lophichthys*, and *Chaunax*, but toothless in *Tetrabrachium* and in the single cleared and stained specimen of *Dibranchus* examined (palatine teeth are present in some ogcocephalid genera and sometimes in *Dibranchus*; Bradbury 1967: 409). In the absence of a mesopterygoid and reduced (or absent) ectopterygoid, the toothless palatine bone of *Brachionichthys* is widely separated from the suspensorium (Figure 23).

Hyoid arch (Figures 9, 10, 21-27).—In *Tetrabrachium* and *Antennarius* (Figures 9, 21) the dorsal head of the quadrate is relatively narrow, somewhat less than the width of the ventral head of the metapterygoid. In contrast, the quadrate of *Lophichthys*, *Brachionichthys*, *Chaunax*, and *Dibranchus* (Figures 22-25) is broad, making a much broader contact with an expanded metapterygoid. In *Dibranchus* the quadrate is exceptionally broad, the anterior half of the dorsal margin coming into contact with the mesopterygoid (Figure 25).

The interhyal of *Antennarius*, *Lophichthys*, and *Brachionichthys* is similar to that of *Tetrabrachium* (but in contrast to that of *Chaunax* and *Dibranchus*; Figures 24, 25) in having a prominent, medial, posterolaterally directed process that wraps around the posterior margin of the respective preopercle when the interhyal rotates upward (Figure 26). This contact between the interhyal and preopercle limits the dorsal rotation of the interhyal and, in turn, limits the extent of abduction of the lower jaw via ligamentous connections with the respective interopercle.

In shape and relative proportions, the branchiostegal rays of *Antennarius*, *Lophichthys*, and *Brachionichthys* are similar to those of *Tetrabrachium*; *Brachionichthys*, however, has lost the anteriormost element in this series (Table 2). In *Chaunax* and *Dibranchus* (Figure 27) the posteriormost branchiostegal ray is greatly enlarged, becoming ankylosed to the ventromedial margin of the subopercle in the later genus.

A small basihyal is present in *Antennarius*, *Tetrabrachium*, *Lophichthys*, and *Chaunax*, but absent in *Brachionichthys* and *Dibranchus*.

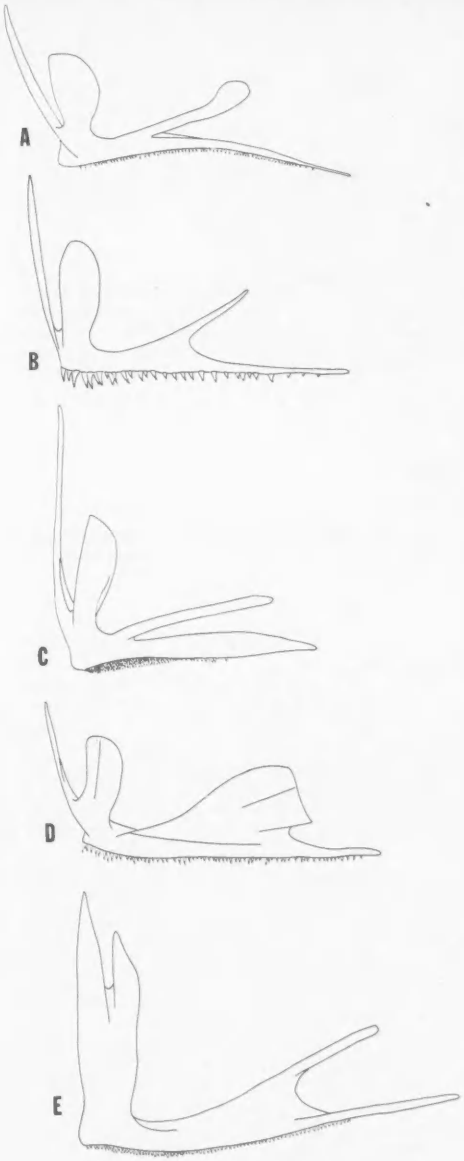

FIGURE 20.—Premaxillae, left lateral views: A. *Antennarius sanguineus*, LACM 8125, 76 mm SL; B. *Lophichthys boschmai*, UW 20773, 47 mm SL; C. *Brachionichthys hirsutus*, AMS IA.6064, 69 mm SL; D. *Chaunax pictus*, UW 20770, 90 mm SL; E. *Dibranchus atlanticus*, MCZ 51257, 105 mm SL.

Opercular apparatus (Figures 9, 21-25).—The opercle and subopercle of *Antennarius*, *Tetrabrachium*, and *Brachionichthys* are similar except in the following details: both elements are considerably reduced in size in *Tetrabrachium* and *Antennarius* (Figures 9, 21); in contrast to the smooth, slightly concave (sometimes deeply incised), posterior margin of the opercle of *Antennarius*, *Tetrabrachium*, and *Lophichthys*, the posterior margin of this bone in *Brachionichthys* is broken into numerous, weakly ossified, bony filaments (Figure 23A); in contrast to the relatively broad, spined subopercle of *Antennarius* and *Lophichthys*, the subopercle of *Tetrabrachium* and *Brachionichthys* (Figures 9, 23A) is a narrow, crescent-shaped element lacking a subopercular spine.

In contrast to the small opercle and subopercle of *Antennarius*, *Tetrabrachium*, *Lophichthys*, and *Brachionichthys*, those of *Chaunax* and *Dibranchus* (Figures 24, 25) are greatly enlarged and expanded posteriorly. A well-developed subopercular spine is present in *Chaunax*, but absent in *Dibranchus*.

The interopercle of *Antennarius*, *Lophichthys*, and *Brachionichthys* (Figures 21-23) is similar to that of *Tetrabrachium*; the interopercle of *Chaunax* and *Dibranchus* (Figures 24, 25) is much more slender and elongate.

Branchial arches (Figures 11, 28-32).—Pharyngobranchial I is represented by a simple, rod-shaped element in *Tetrabrachium*, *Antennarius*, and *Lophichthys* (Figures 11, 28, 29). In the single specimen of *Chaunax* examined pharyngobranchial I is Y-shaped (Figure 31). This element is toothless in *Antennarius*, *Tetrabrachium*, and *Chaunax*, but bears a series of approximately eight small teeth in *Lophichthys* (Figure 29). Pharyngobranchial I is absent in *Brachionichthys* and *Dibranchus*. Pharyngobranchial IV is absent in all antennarioids.

In *Tetrabrachium*, *Antennarius*, and *Lophichthys* (Figures 11, 28, 29), epibranchial I is triradiate in shape, toothless in *Antennarius* and *Tetrabrachium*, but bearing a single row of about 13 small teeth in *Lophichthys* (Figure 29). A similarly shaped epibranchial I, associated with three and two tooth plates is present in *Chaunax* and *Dibranchus*, respectively (Figures 31, 32). An L-shaped epibranchial I, associated with a single tooth plate, is present in *Brachionichthys* (Figure

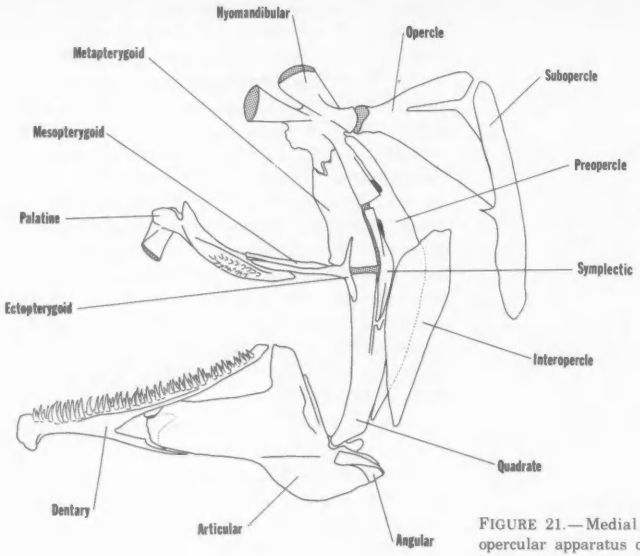

FIGURE 21.—Medial view of lower jaw, suspensorium, and opercular apparatus of *Antennarius sanguineus*, LACM 8125, 76 mm SL.

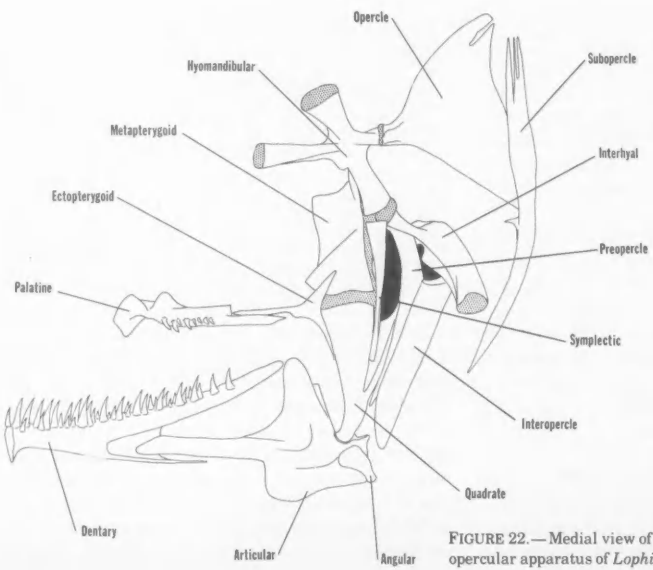

FIGURE 22.—Medial view of lower jaw, suspensorium, interhyal, and opercular apparatus of *Lophichthys boschmai*, UW 20773, 47 mm SL.

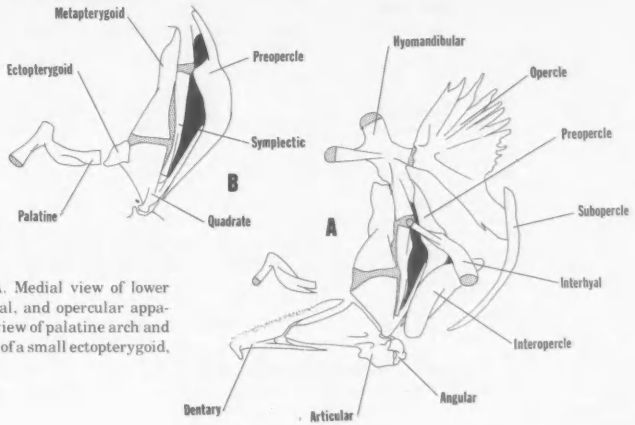

FIGURE 23.—*Brachionichthys hirsutus*: A. Medial view of lower jaw, palatine bone, suspensorium, interhyal, and opercular apparatus, AMS IA.6064, 69 mm SL; B. Medial view of palatine arch and suspensorium, right side, showing presence of a small ectopterygoid, UW 20769, 42 mm SL.

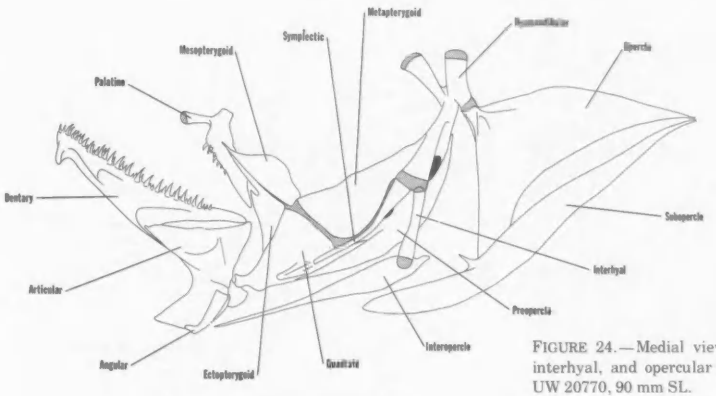

FIGURE 24.—Medial view of lower jaw, suspensorium, interhyal, and opercular apparatus of *Chaunax pictus*, UW 20770, 90 mm SL.

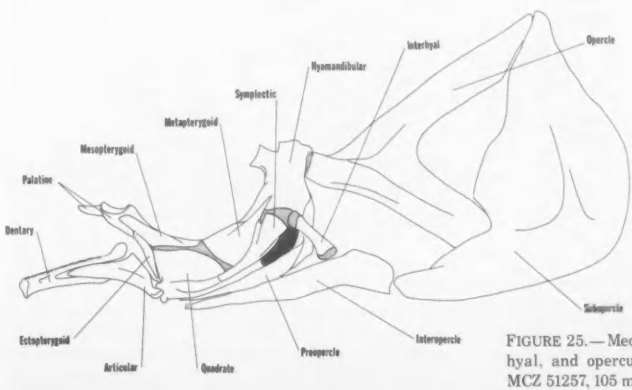

FIGURE 25.—Medial view of lower jaw, suspensorium, interhyal, and opercular apparatus of *Dibranchus atlanticus*, MCZ 51257, 105 mm SL.

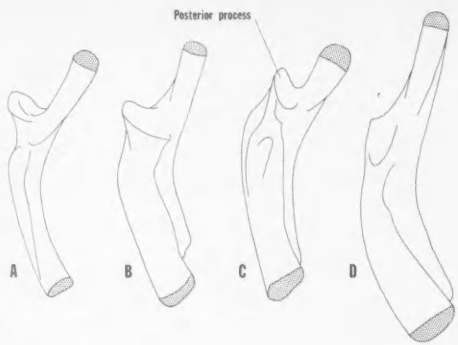

FIGURE 26.—Lateral view of interhyal, right side: A. *Antennarius sanguineus*, LACM 8125, 76 mm SL; B. *Tetrabrachium ocellatum*, AMS IB.7178, 61 mm SL; C. *Lophichthys boschmai*, UW 20773, 47 mm SL; D. *Brachionichthys hirsutus*, AMS IA.6064, 69 mm SL.

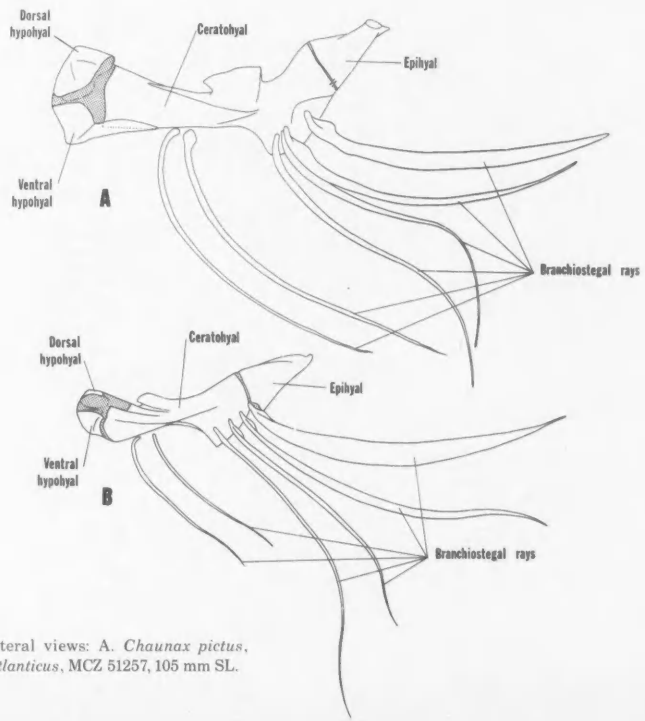

FIGURE 27.—Hyoid apparatus, left lateral views: A. *Chaunax pictus*, UW 20770, 90 mm SL; B. *Dibranchus atlanticus*, MCZ 51257, 105 mm SL.

TABLE 2.—Characters of representative genera of the major subgroups of the Antennarioidei.

Item	*Antennarius*	*Tetrabrachium*	*Lophichthys*	*Brachionichthys*	*Chaunax*	*Dibranchus*
Branchiostegal rays	2+4	2+4	2+4	1+4	2+4	2+4
Pharyngobranchial I	rod shaped (toothless)	rod shaped (toothless)	rod shaped (toothed)	absent	forked (toothless)	absent
Palatine teeth	present	absent	present	absent	present	absent
Epibranchial teeth						
Arch I	absent	absent	single row	1 plate	3 plates	2 plates
Arch III	absent	absent	absent	absent	absent	1 plate
Ceratobranchial teeth						
Arch I	absent	absent	absent	2 plates	present	present
Arch II	absent	absent	absent	1 plate	present	present
Arch III	absent	absent	absent	1 plate	present	present
Arch IV	absent	absent	absent	absent	present	present or absent
Hypobranchial II	bifurcated	bifurcated	bifurcated	simple	simple	absent
Hypobranchial III	bifurcated	bifurcated	bifurcated	simple	simple	absent
Pseudobranch	present	absent	absent	absent	absent	absent
Swim bladder	present	absent	absent	absent	absent	absent
Basihyal	present	present	present	absent	present	absent
Vertebrae (precaudal)	19(4)	22(4)	19(4)	22(4)	19(4)	19(6)
Epural	1	0	remnant present or absent	0	1	1
Dorsal fin rays	11-15	16-17	12-13	17	12	5
Anal fin rays	6-9	11-12	9	7	7	4
Pectoral fin radials	3	3	3	2	3	3
Pectoral fin rays	7-14	4+5	7	8	14	14
Pelvic fin rays	I+5	I+5	I+5	I+4	I+4	I+5

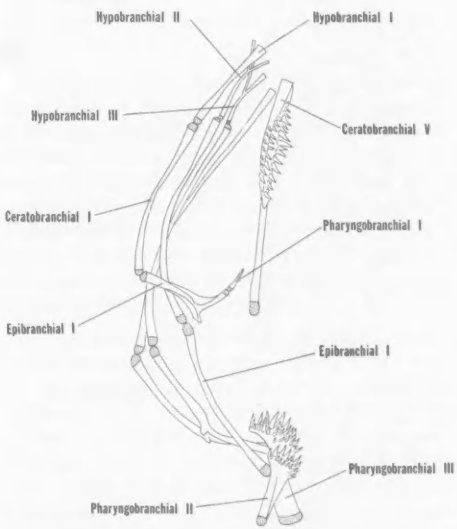

FIGURE 28.—Branchial arches of *Antennarius sanguineus*, LACM 8125, 76 mm SL. The ventral portion of the branchial basket is shown in dorsal view, the dorsal portion (epibranchials and pharyngobranchials) is folded back and shown in ventral view.

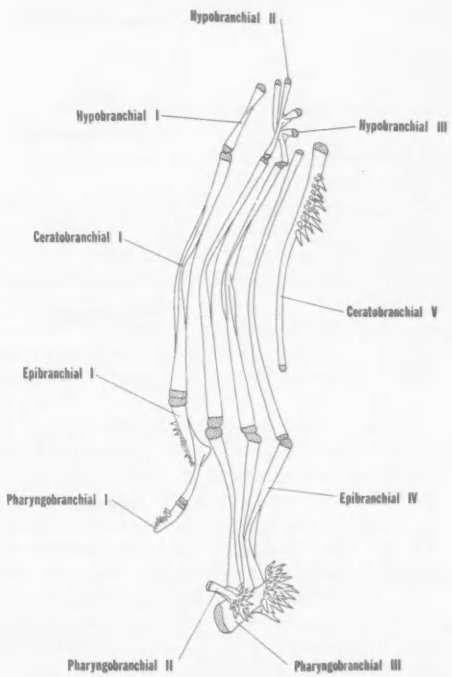

FIGURE 29.—Branchial arches of *Lophichthys boschmai*, UW 20773, 47 mm SL. The ventral portion of the branchial basket is shown in dorsal view, the dorsal portion (epibranchials and pharyngobranchials) is folded back and shown in ventral view.

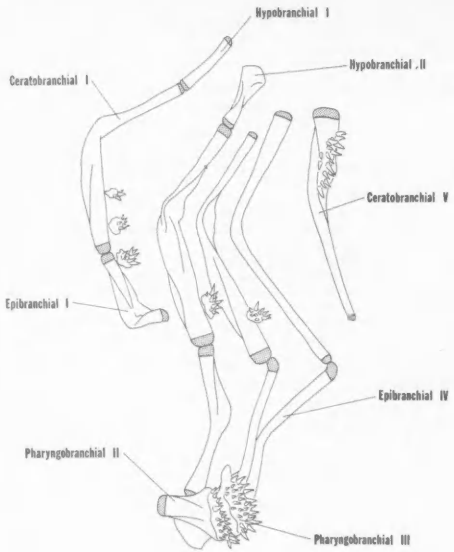

FIGURE 30.—Branchial arches of *Brachionichthys hirsutus*, AMS IA.6064, 69 mm SL. The ventral portion of the branchial basket is shown in dorsal view, the dorsal portion (epibranchials and pharyngobranchials) is folded back and shown in ventral view.

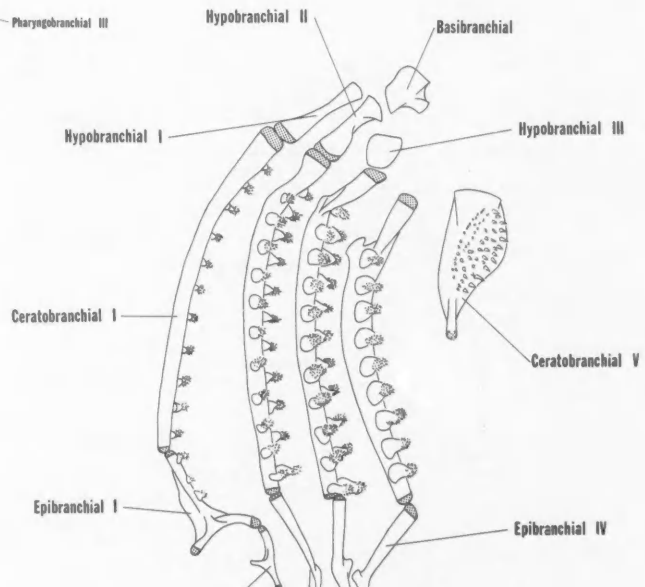

FIGURE 31.—Branchial arches of *Chaunax pictus*, UW 20770, 90 mm SL. The ventral portion of the branchial basket is shown in dorsal view, the dorsal portion (epibranchials and pharyngobranchials) is folded back and shown in ventral view.

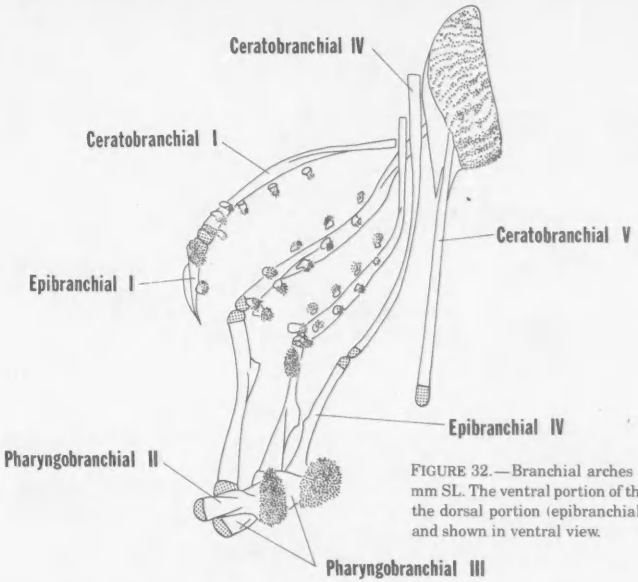

FIGURE 32.—Branchial arches of *Dibranchus atlanticus*, MCZ 51257, 105 mm SL. The ventral portion of the branchial basket is shown in dorsal view, the dorsal portion (epibranchials and pharyngobranchials) is folded back and shown in ventral view.

30). Epibranchial III is toothless in all antennarioids examined except in *Dibranchus* (Figure 32) where this bone is associated with a single tooth plate.

Ceratobranchials I through IV are toothless in *Tetrabrachium*, *Antennarius*, and *Lophichthys* (Figures 11, 28, 29). In *Brachionichthys* (Figure 30), one to three tooth plates are present on ceratobranchials I through III; in *Chaunax* (Figure 31), tooth plates are present on ceratobranchials I through IV; in *Dibranchus* (Figure 32), tooth plates are present on ceratobranchials I through III (but also sometimes present on ceratobranchial IV, see Bradbury 1967:408) (Table 2).

In contrast to the separate, individual teeth present on pharyngobranchial I and epibranchial I of *Lophichthys* (Figure 29), those present on epibranchial I and ceratobranchials I through IV of *Brachionichthys*, *Chaunax*, and *Dibranchus* (Figures 30-32) are born in clusters on individual tooth plates. The tooth plates of *Chaunax* and *Dibranchus* (Figures 31, 32) (and a number of other ogcocephalid taxa, see Bradbury 1967) differ from those of *Brachionichthys* (Figure 30) and from those of all other lophiiforms in being raised, pedicallike structures bearing a cluster of numerous, tiny teeth at the apex (but see Bradbury 1967, fig. 7, for other forms of gill teeth in ogcocephalids).

Ceratobranchial V is well toothed in all antennarioids examined. In *Tetrabrachium*, *Antennarius*, *Lophichthys*, and *Brachionichthys* (Figures 11, 28-30), this bone consists of a narrow, toothed proximal portion and a tapering, cylindrical distal portion; in *Chaunax* (Figure 31) only a triangular, toothed portion is present. In *Dibranchus* (Figure 32), ceratobranchial V is greatly enlarged, consisting of a finely toothed, expanded proximal portion and a long, cylindrical distal shaft.

Hypobranchial I of *Tetrabrachium*, *Antennarius*, *Lophichthys*, *Brachionichthys*, and *Chaunax* (Figures 11, 28-31) and hypobranchial II of *Brachionichthys* and *Chaunax* (Figures 30, 31) are simple, rod-shaped bones. Hypobranchials II and III of *Tetrabrachium*, *Antennarius*, and *Lophichthys* (Figures 11, 28, 29) are bifurcated proximally (this feature is probably plesiomorphic for lophiiforms since a similar situation is present in all batrachoidids examined). Hypobranchial III is absent in *Brachionichthys* (Figure 30), but represented by a semicircular ossification in *Chaunax* (Figure 31). There are no ossified hypobranchials in the single specimen of *Dibranchus* examined (Figure 32, Table 2).

Basibranchials are represented by a single ossification in *Chaunax* (Figure 31), but are absent in *Antennarius*, *Tetrabrachium*, *Lophichthys*, *Brachionichthys*, and *Dibranchus*.

Gill filaments are absent on arch I of *Chaunax* and *Dibranchus*. Filaments are present as holobranchs on arch I of *Antennarius*, *Tetrabrachium*, *Lophichthys*, and *Brachionichthys*, and on arches II and III of all antennarioids examined. Hemibranchs are present on arch IV of all antennarioids examined (filaments may sometimes be absent on arch IV of *Dibranchus*; Bradbury 1967:408).

A small pseudobranch is present in *Antennarius*, but absent in all other antennarioids examined.

Vertebrae and caudal skeleton (Figures 12, 33-35).—The vertebral column of *Antennarius*, *Lophichthys*, and *Brachionichthys* (Figures 33, 34A) is similar to that of *Tetrabrachium* (Figure 12) in having the neural spines of three to four anterior vertebrae (preural centra 11-13 in *Antennarius*, Figure 33; 14-17 in *Tetrabrachium*, Figure 12; 12-14 in *Lophichthys*, Figure 34A; and 15-18 in *Brachionichthys*) short (spatulate in all antennarioids examined except for *Lophichthys*, *Chaunax*, *Dibranchus*, and a few specialized antennariid genera, i.e., *Echinophryne*, *Trichophryne*, and *Rhycherus*; see Appendix) and not interdigitating with the corresponding proximal radials of the overlying soft dorsal fin (this feature appears to be plesiomorphic for the Lophiiformes being more or less developed in nearly all taxa).

In *Chaunax* (Figure 35A), the neural spines are similar throughout the length of the axial skeleton. In *Dibranchus* (Figure 35B), the vertebral column and caudal skeleton are strongly modified for a benthic life-style. The neural and haemal spines of all centra are short and broad. Preural centra 14 through 18 are considerably more elongate than the remaining centra; the neural spines of these centra are expanded anteroposteriorly and compressed laterally to form a solid bony partition along the dorsal midline. Mobility in this region of the axial skeleton is severely reduced due to large, overlapping prezygapophyses (considerable movement is retained, however, between the two anteriormost centra, preural centra 18 and 19).

In both specimens of *Lophichthys* examined a peculiar bridging of bone is present between the distal tips of the haemal spines of the 14th through the 16th preural centra (Figure 34A). This kind of ossification has not been described for any other lophiiform.

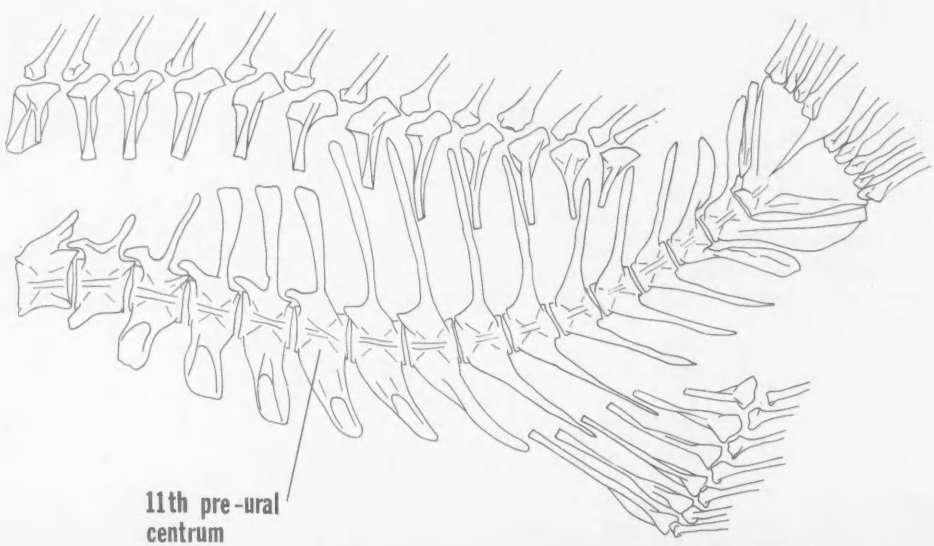

FIGURE 33.—Vertebrae, caudal skeleton, and median fins of *Antennarius sanguineus*, LACM 8125, 76 mm SL.

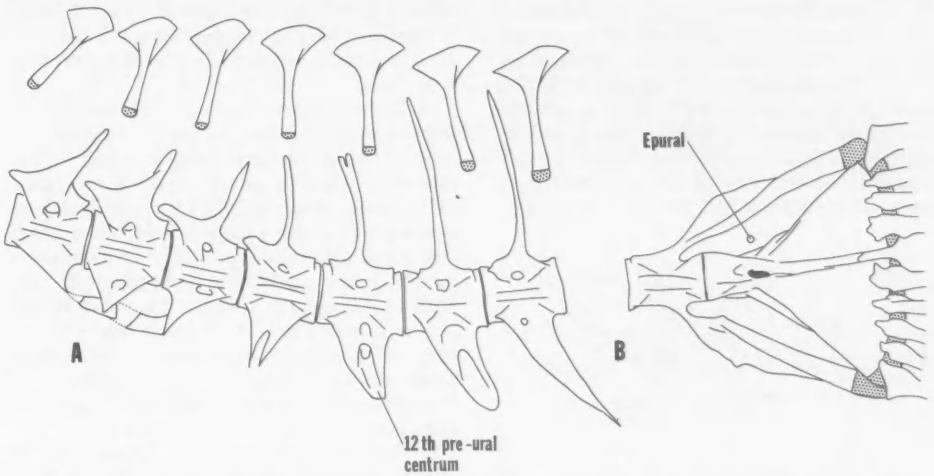

FIGURE 34.—*Lophichthys boschmai*, UW 20773, 47 mm SL: A. Preural centra 12 through 16, showing partially ossified connection between distal tips of haemal spines of preural centra 14 through 16; B. Caudal skeleton showing remnant of epural.

A single epural is present in *Antennarius*, *Chaunax*, and *Dibranchus* (Figures 33, 35) (oval and laterally compressed in the later genus). In the larger (47 mm) of the two specimens of *Lophichthys* (Figure 34B) examined, the epural is represented by a tiny circular ossification. No trace of this element is present in the smaller (44 mm) individual of *Lophichthys*, or in any other antennarioid examined.

Axial skeletal elements of the antennarioid taxa examined are compared in Table 2.

Medial fins and illicial apparatus (Figures 13, 36-39).—The spinous dorsal fin of *Tetrabrachium*,

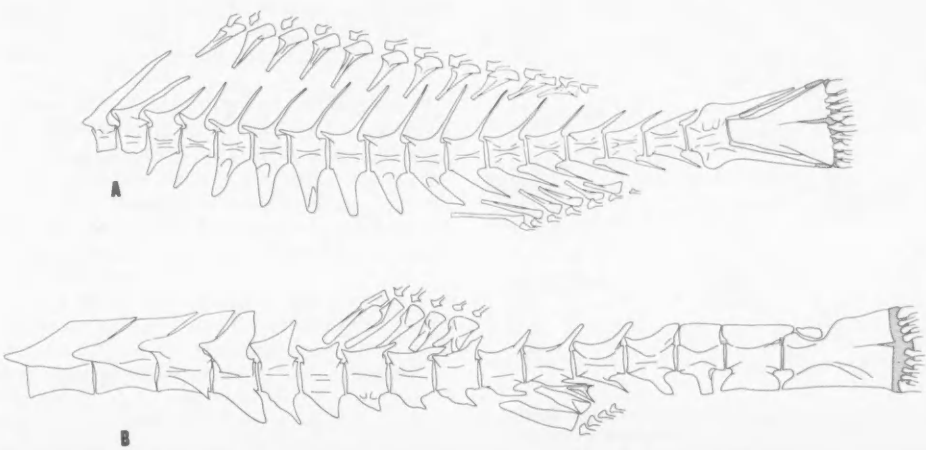

FIGURE 35.—Vertebrae, caudal skeleton, and median fins: A. *Chaunax pictus*, UW 20770, 90 mm SL; B. *Dibranchus atlanticus*, MCZ 51257, 105 mm SL.

Antennarius, *Brachionichthys*, *Lophichthys*, and *Chaunax* consists of three spines. In *Antennarius*, *Brachionichthys*, and *Lophichthys* (Figures 36, 37) all three spines are well developed, extending above the skin of the head. In many species of *Antennarius* spines II and III are membranously attached posteriorly to the head; in *Brachionichthys*, and in some forms of *Antennarius* (e.g. *A. pauciradiatus* Schultz 1957:100, fig. 7; *A. randalli* Allen 1970:518, fig. 1, 2a), spine II is membranously attached to the full length of spine III, and spine III is, in turn, membranously attached posteriorly to the head.

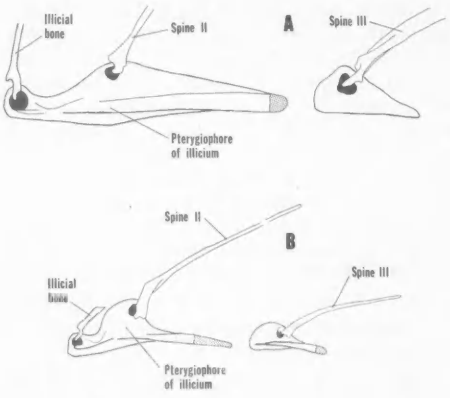

FIGURE 36.—Spinous dorsal fin, left lateral view: A. *Antennarius sanguineus*, LACM 8125, 76 mm SL; B. *Brachionichthys hirsutus*, AMS IA.6064, 69 mm SL.

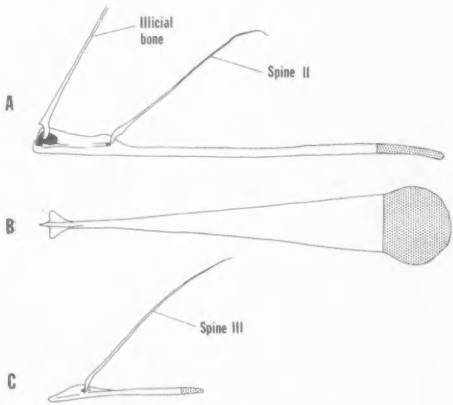

FIGURE 37.—Elements of spinous dorsal fin of *Lophichthys boschmai*, UW 20773, 47 mm SL: A. Anteriormost pterygiophore bearing illicial bone and dorsal spine II, left lateral view; B. Anteriormost pterygiophore, ventral view; C. Second pterygiophore bearing dorsal spine III, left lateral view.

In *Tetrabrachium* (Figure 13), all three dorsal fin spines are evident externally, but all are reduced in size; the greater part of spine III is covered by skin of the head, only the tip emerging. In *Chaunax* (Figure 38A), all three dorsal fin spines are relatively well developed, but spines II and III are laid back on the surface of the cranium completely covered by skin and apparently nonfunctional (a similar situation is found in *Histiophryne*, a highly specialized genus of the Antennariidae). The illicial bone (dorsal spine I), when retracted, comes to lie within an aperture on the face between the nostrils and eyes, called the illicial cavity (Figure 39A; Bradbury 1967).

In *Dibranchus* (Figure 38B), dorsal spine III and its pterygiophore are absent. Spine II is reduced to a small vestige of bone (the "H-shaped" bone of Bradbury 1967:402, fig. 1) lying on, or often fused to the anteriormost pterygiophore just behind the articulation of the pterygiophore and the illicial bone. As in *Chaunax*, the illicial bone, when retracted, comes to lie within an illicial cavity (Figure 39B, C).

In *Tetrabrachium*, *Antennarius*, *Lophichthys*, and *Brachionighthys* (Figures 13, 36-37), the anteriormost pterygiophore that supports the illicial bone and dorsal spine II, and the second pterygiophore that supports dorsal spine III have highly compressed, bladelike dorsal expansions. Each

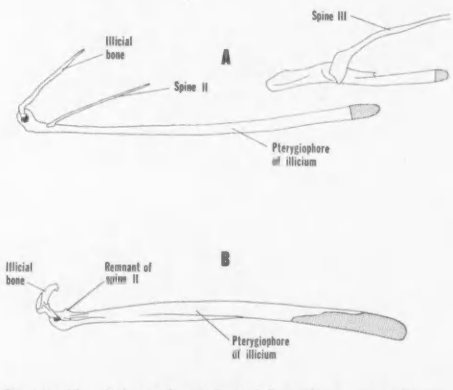

FIGURE 38.—Spinous dorsal fin, left lateral views: A. *Chaunax pictus*, UW 20770, 90 mm SL; B. *Dibranchus atlanticus*, MCZ 51257, 105 mm SL.

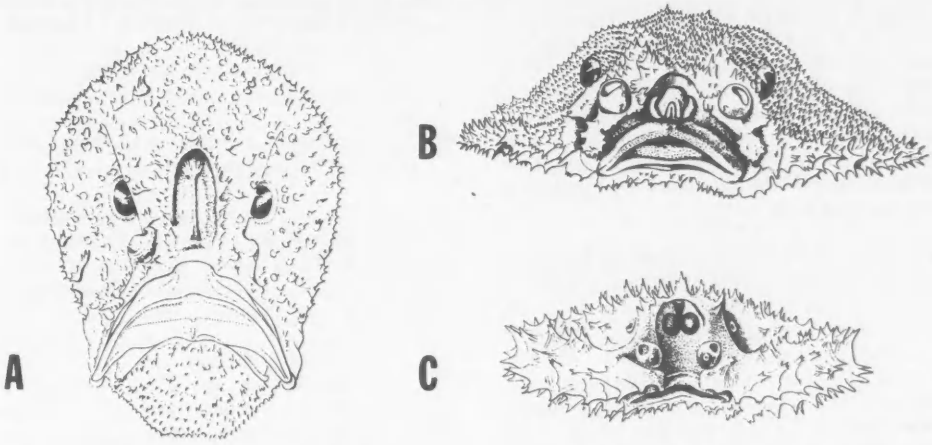

FIGURE 39.—Anterior views showing illicial cavity within which the illicial bone, when fully retracted, comes to lie: A. *Chaunax coloratus* Garman; B. *Dibranchus spinosa* (Garman); C. *Halieutopsis tumifrons* (Garman). After Garman (1899).

expansion is pierced by a large, circular foramen within which fits the bifurcated proximal end of the respective dorsal fin spine. The anteriormost pterygiophore of *Lophichthys* (Figure 37A, B) is unique among the antennarioids examined in being much more elongate, and in becoming greatly depressed and laterally expanded posteriorly. In *Chaunax* and *Dibranchus* (Figure 38), the pterygiophores of the dorsal fin spines are cylindrical in cross section along their entire length.

Dorsal and anal fin ray counts of the antennarioids examined are compared in Table 2.

Pectoral and pelvic girdles and fins (Figures 14, 40).—The posttemporal of *Antennarius*, *Lophichthys*, *Brachionichthys*, and *Chaunax* is similar to that of *Tetrabrachium*, attached to the cranium in such a way that considerable movement in an anterodorsal-posteroventral plane is possible. In contrast, the posttemporal of *Dibranchus* is fused to the cranium.

The number and length of the pectoral fin radials varies somewhat among the antennarioids examined. There are three relatively short pectoral radials in *Tetrabrachium*, and *Antennarius* (Figures 14, 40A). The three radials of *Lophichthys* (Figure 40B) are exceptionally long and narrow; the second radial is reduced, tapering proximally to a slender filament. *Brachionichthys* (Figure 40C) has two, somewhat elongate pectoral

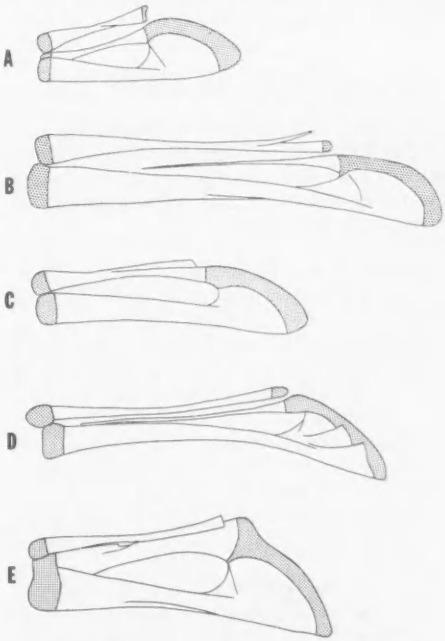

FIGURE 40.—Pectoral radials, lateral view, left side: A. *Antennarius striatus*, UW 20768, 67 mm SL; B. *Lophichthys boschmai*, UW 20773, 47 mm SL; C. *Brachionichthys hirsutus*, AMS IA.6064, 69 mm SL; D. *Chaunax pictus*, UW 20770, 90 mm SL; E. *Dibranchus atlanticus*, MCZ 51257, 105 mm SL.

radials. In the single osteological preparation of *Chaunax* examined (Figure 40D), there are three separate, relatively long radials, but the ventralmost element appears to be the result of fusion of three, perhaps indicating the presence of a total of five radials. In *Dibranchus* (Figure 40E) there are three, relatively short radials, the dorsalmost two lying side-by-side and fused to one another at their proximal and distal ends.

Skin spines.—Numerous, close-set dermal spines cover the head and body of *Antennarius*, *Lophichthys*, *Brachionichthys*, and *Chaunax*; the spines are bifurcated in *Antennarius*, but simple in *Lophichthys*, *Brachionichthys*, and *Chaunax*. Dermal spines are absent in *Tetrabrachium*, except for the occasional presence of a spinule associated with an individual pore of the acousticolateralis system. The head and body of *Dibranchus* are nearly totally enclosed in a covering of thick, nonoverlapping tubercles (Bradbury 1967:404).

PHYLOGENETIC RELATIONSHIPS

The order Lophiiformes is an assemblage of 18 families, 59 genera, and approximately 255 living species of marine teleosts, the monophyletic origin of which seems certain based on the following list of synapomorphic features:

1) Spinous dorsal fin primitively of six spines, the anteriormost three of which are cephalic in position and modified to serve as a luring apparatus (involving numerous associated specializations, e.g., a medial depression of the anterior portion of the cranium, loss of the nasal bones [nasal of Rosen and Patterson 1969 = lateral ethmoid] and supraoccipital lateral-line commissure, and modifications of associated musculature and innervation);
2) Epiotics separated from parietals and meeting on the midline posterior to the supraoccipital;
3) Gill opening restricted to a small, elongate tubelike opening situated immediately dorsal to, posterior to, or ventral to (rarely partly anterior to) pectoral fin base;
4) Second ural centrum fused with the first ural and first preural centra to form a single hypural plate (sometimes deeply notched posteriorly) that emanates from a single, complex half-centrum (Rosen and Patterson 1969:441, text fig. 4E, 60);
5) Pectoral radials narrow and elongate, the ventralmost radial considerably expanded distally;
6) Eggs spawned in a double, scroll-shaped mucous sheath (Rasquin 1958).

Since Regan (1912), three major lophiiform taxa of equal rank have been recognized by nearly all authors. These taxa, together with their currently recognized families (the 11 families of the bathypelagic Ceratioidei excluded), are:

Suborder Lophioidei
  Family Lophiidae
Suborder Antennarioidei
  Family Antennariidae
  Family Brachionichthyidae
  Family Chaunacidae
  Family Ogcocephalidae
Suborder Ceratioidei

In attempting to place *Tetrabrachium* within the framework of this classification it became apparent that not all of the relationships expressed can be supported by an adherence to cladistic methodology. Although never questioned by any subsequent author, the monophyly of each of Regan's (1912) three major lophiiform taxa has not been established. Serious problems lie within the Antennarioidei: a number of synapomorphic features support a sister-group relationship between the Antennariidae and Brachionichthyidae (see below), and between the Chaunacidae and Ogcocephalidae, but no convincing synapomorphy is known at the present time that will link these two larger subgroups. Thus, the problems of interpreting the interrelationships of higher taxonomic categories within the Antennarioidei, and the relationships of this suborder to the Lophioidei and Ceratioidei are postponed. The following discussion is limited for the most part to *Tetrabrachium* and its relationship to the Antennariidae, to *Lophichthys* (here given familial rank as suggested by Boeseman 1964), and to the Brachionichthyidae. Synapomorphic features that establish monophyly for a group containing the Chaunacidae and Ogcocephalidae are also enumerated. The relative primitiveness of the character states utilized below was determined by examining their distribution among all available lophiiform material (47 of the 59 currently recognized genera;

material unavailable for comparison includes the lophioid genus *Sladenia* Regan, seven of the nine ogcocephalidid genera, and a number of rare and highly derived ceratioid genera), as well as representative taxa of the Batrachoidiformes (3 of the 12 nominal genera), the only group bearing evidence of sister-group relationship with the Lophiiformes (Regan 1912; Gregory 1933; Rosen and Patterson 1967) (see Appendix).

Antennarius, used here as the representative taxa of the Antennariidae, is recognized as the least derived genus of the family based on a comparative anatomical study of some eight nominal antennariid genera (Pietsch in prep., see Appendix). Except for synapomorphies that establish monophyly for *Antennarius*, all known characters of taxonomic importance found among the eight genera are present in *Antennarius* in the primitive state. For example, a mesopterygoid and an epural are present in *Antennarius* but absent in all other genera except *Histrio*; *Histrio* is clearly derived relative to *Antennarius* in having enlarged pelvic fins, a pectoral fin lobe that is detached from the body along most of its length, absence of skin spines, and a unique pelagic habitat in sargassum weed. Similarly, each of the remaining six antennariid genera possesses a number of autapomorphic features that indicate its derived nature relative to *Antennarius*. Although these and other data support the least derived position of *Antennarius*, this verification is not basic to the subsequent discussion of relationships since the synapomorphic features used to establish the sister groups proposed below are synapomorphic for all eight antennariid genera.

Tetrabrachium is most closely related cladistically to *Antennarius*, and is here classified on this basis as a sister-family, the Tetrabrachiidae (first proposed by Whitley 1935), of the Antennariidae (Figure 41). This hypothesis of relationship is supported by three synapomorphies:

1) Posteromedial process of vomer emerging from ventral surface as a laterally compressed, keellike structure, its ventral margin (as seen in lateral view) strongly convex (this character state is present in *Tetrabrachium* and in all antennariid taxa examined; in the batrachoidids and other lophiiforms examined the posteromedial process is flush with the ventral surface of the vomer, its ventral margin straight to slightly concave);
2) Postmaxillary process of premaxilla spatulate (this character state is present in *Tetrabrachium* and in all antennariid taxa examined; in the batrachoidids and other lophiiforms examined the postmaxillary process of the premaxilla is connected to the toothed portion of this element by bone, represented by a narrow, tapering structure, or absent);
3) Opercle similarly reduced in size (in *Tetrabrachium* and all antennariid taxa examined the width of the opercle is approximately $\leq 25\%$ the length of the suspensorium; in the batrachoidids and other lophiiforms examined this distance is $>40\%$).

Although the classification of taxa presented here is based on recency of common descent, the amount and nature of evolutionary change between the Antennariidae and the Tetrabrachiidae is an important part of their evolutionary histories. That the Tetrabrachiidae has entered a "new adaptive zone" relative to the Antennariidae is evidenced morphologically by a number of unique, derived features: eyes small, close set, protruding from the dorsal surface of the head; mouth small, superior, lower lip fringed with small cutaneous papillae; illicial apparatus reduced; pectoral fin double, the ventral portion membranously attached to the side of the body; and pectoral fin lobe membranously attached to the rays of the pelvic fin. The webbing between the pectoral fin and the body, and between the pectoral and pelvic fins is apparently used to remove soft-bottom substrate (fine sand or mud) from beneath by scooping material away in a lateral direction and simultaneously throwing material up and over to cover the animal; the fringed lip allows for intake of water while helping to prevent particles from entering the pharyngeal cavity. These and other characters listed above reflect a life style similar to that of a uranoscopid or synanceiid, lying for long periods of time buried up to the eyes in sand or mud, a mode of existence unlike that of any other antennarioid.

The results of this study further show that the Antennariidae and Tetrabrachiidae together form the primitive sister group of the Lophichthyidae and that these three taxa together form the primitive sister group of the Brachionichthyidae (Figure 41). The monophyly of a group including the Antennariidae, Tetrabrachiidae, and Lophichthyidae is supported by a single synapomorphy:

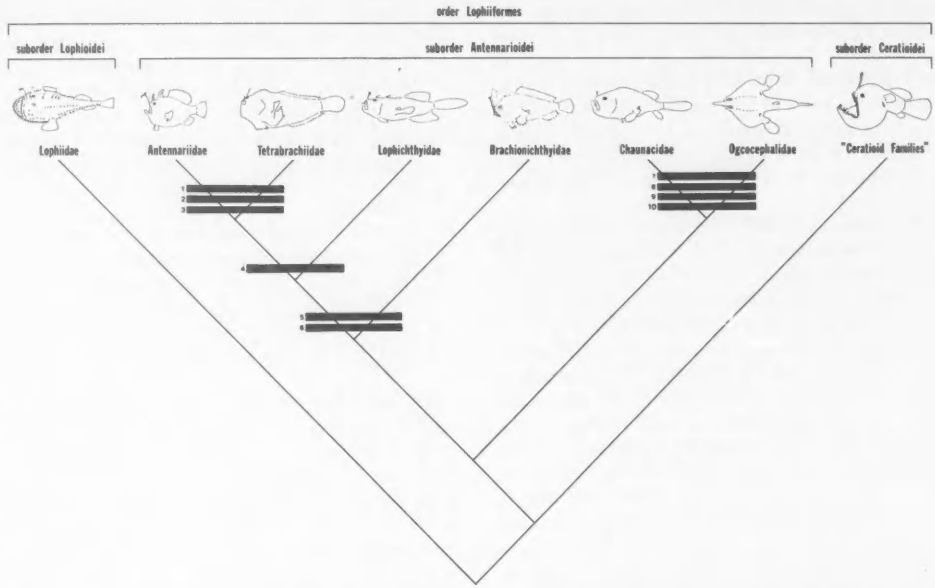

FIGURE 41.—Cladogram showing proposed phylogenetic relationships of major subgroups of the Lophiiformes. Note that not all sister-group relationships are supported by sufficient data. Black bars and numbers refer to synapomorphic features discussed in the text: 1) Posteromedial process of vomer emerging from ventral surface as a laterally compressed, keellike structure; 2) Postmaxillary process of premaxilla spatulate; 3) Opercle reduced; 4) Ectopterygoid triradiate; 5) Interhyal with a medial, posterolaterally directed process; 6) Illicial pterygiophore and pterygiophore of third dorsal fin spine with highly compressed, bladelike dorsal expansions; 7) Posterior-most branchiostegal ray exceptionally large; 8) Gill teeth tiny, arranged in a tight cluster at apex of pedicellike tooth plates; 9) Gill filaments of gill arch I absent; 10) Illicial bone, when retracted, lying within an illicial cavity. Drawings courtesy of The American Museum of Natural History.

4) Ectopterygoid triradiate, a dorsal process overlapping the medial surface of the metapterygoid (this character state is present in *Tetrabrachium*, *Lophichthys*, and all antennariids examined; in the batrachoidids and other lophiiforms examined this element is crescent shaped, making no contact with the metapterygoid).

That the Antennariidae, Tetrabrachiidae, Lophichthyidae, and Brachionichthyidae constitute a monophyletic group is supported by two synapomorphies:

5) Interhyal with a medial, posterolaterally directed process that comes into contact with the respective preopercle (this character state *is present in Tetrabrachium*, *Lophichthys*, *Brachionichthys*, and all antennariids examined; in the batrachoidids and all other lophiiforms examined this interhyal process is absent);
6) Illicial pterygiophore and pterygiophore of the third dorsal fin spine with highly compressed, bladelike dorsal expansions (this character state is present in *Tetrabrachium*, *Lophichthys*, *Brachionichthys*, and all antennariids examined; in other lophiiforms examined these dorsal expansions are absent; this character does not extend to batrachoidids).

Gregory (1933:388, fig. 264) speculated that the membranous connection between the spines of the dorsal fin of *Brachionichthys* represents a primitive feature: "This is the most primitive condition among the typical pediculates" (= lophiiforms). On this assumption, in addition to a statement that the skeleton of *Brachionichthys* is relatively primitive in appearance, Gregory (1933:387) concluded that "...*Brachionichthys* is much less spe-

cialized [relative to antennariids and lophiids] and in fact seems to give several clues to the origin of the entire order." On the contrary, all evidence indicates that a membranous connection between the dorsal fin spines is apomorphic for anglerfishes; of the approximately 255 living species of the order this feature is present in the four nominal species of *Brachionichthys* and in two of the most derived species of the genus *Antennarius* (*A. pauciradiatus* and *A. randalli*; Pietsch in prep.). Besides this character, *Brachionichthys* possesses a set of autapomorphic features that clearly remove it from consideration as "the most primitive lophiiform." In addition to those autapomorphies listed in the analytical key below, Winterbottom (1974:284) has identified an apparently unique derived condition of the inclinator dorsales muscle of the second dorsal fin spine of *Brachionichthys*.

Although strikingly dissimilar at first glance, a number of synapomorphies support a hypothesis of sister-group relationship between the families Chaunacidae and Ogcocephalidae (Figure 41):

7) Posteriormost branchiostegal ray exceptionally large (in batrachoidids and all other lophiiforms examined the size of the posteriormost branchiostegal does not differ significantly from the adjacent branchiostegal);
8) Gill teeth tiny, arranged in a tight cluster at apex of pedicellike tooth plates (in batrachoidids and other lophiiforms examined the gill teeth are relatively large, and either single, or associated with a flat, rounded tooth plate);
9) Gill filaments of gill arch I absent (in batrachoidids and all other lophiiforms examined gill filaments are present on arch I);
10) Illicial bone, when retracted, lying within an illicial cavity (an illicial cavity is absent in all other lophiiforms examined; this character does not extend to batrachoidids).

Historically, chaunacids and ogcocephalids have been classified with antennariids and brachionichthyids by aspects of general similarity (i.e., they neither look like lophioids or ceratioids). Nearly all of these similarities are easily identified as character states that are plesiomorphic for antennarioids (or for lophiiforms as a whole); the synapomorphic nature of the few remaining similarities is unresolvable. Thus, despite a thorough osteological search, this study has failed to identify the sister group of a group including the Chaunacidae and Ogcocephalidae among the known members of the Lophiiformes. In the absence of any evidence for or against, these taxa are tentatively retained within the Antennarioidei (Figure 41).

Of the possible cladograms that could be constructed on the basis of the data provided in this study, the one shown in Figure 41 involves the least number of convergences. The preferred phylogeny requires four cases of convergence (Table 2), all of which, however, are loss characters that extend to other lophiiform taxa:

1) the independent loss of palatine teeth in the Tetrabrachiidae and Brachionichthyidae [also absent in some ogcocephalids (see Bradbury 1967:409) and in all ceratioids];
2) the independent loss of a pseudobranch in the Tetrabrachiidae, Lophichthyidae, and Brachionichthyidae (also absent in chaunacids, ogcocephalids, and all ceratioids);
3) the independent loss of the swim bladder in the Tetrabrachiidae, Lophichthyidae, and Brachionichthyidae (also absent in lophioids, chaunacids, ogcocephalids, and ceratioids);
4) the independent loss of the epural in the Tetrabrachiidae and Brachionichthyidae also absent in all antennariid genera examined except *Antennarius*, *Antennatus*, and *Histrio*; [although present in the Caulophrynidae (Pietsch 1979, fig. 11), the epural is absent in all other ceratioids].

Plesiomorphic and autapomorphic features of the major subgroups of the Antennarioidei are incorporated into the following analytical key:

1A. Spinous dorsal of three spines, emerging from dorsal surface of cranium, illicium not retractable within an illicial cavity; ectopterygoid present or absent, interopercle flat and broad 2
1B. Spinous dorsal of one spine (spines II and III reduced and embedded beneath skin of head or lost), illicium retractable within an illicial cavity; ectopterygoid present, crescent shaped; interopercle elongate and narrow 5
2A. Parietals well separated by supraoccipital; ectopterygoid triradiate; ceratobranchials I through IV toothless; hypobranchials II and III bifurcated prox-

imally; three pectoral radials; pelvic fin of one spine and five rays 3

2B. Parietals meeting on the midline dorsal to supraoccipital; ectopterygoid roughly oval in shape or absent; ceratobranchials I through III with one or more tooth plates; hypobranchial II simple, hypobranchial III absent; two pectoral radials; pelvic fin of one spine and four rays ..... Brachionichthyidae

3A. Vomer narrow, width between lateral ethmoids considerably less than between lateral margins of sphenotics; dorsal head of quadrate narrow, width less than that of metapterygoid; postmaxillary process of premaxilla spatulate; opercle reduced in size; pharyngobranchial and epibranchial of first arch toothless; bony connection between tips of haemal spines absent; pterygiophore of illicium short, posterior end cylindrical 4

3B. Vomer wide, width between lateral ethmoids nearly as great as between lateral margins of sphenotics; dorsal head of quadrate broad, width equal to or greater than that of metapterygoid; postmaxillary process of premaxilla tapering to a point; opercle expanded posteriorly; pharyngobranchial and epibranchial of arch I toothed; bony connection between tips of haemal spines of 14th through 16th preural centra; pterygiophore of illicium elongate, greatly depressed and laterally expanded posteriorly ..... Lophichthyidae

4A. Eyes lateral, dorsal fin spines well developed; mouth large; pectoral fin single, rays not membranously attached to side of body; pectoral fin lobe not membranously attached to rays of pelvic fin; soft dorsal fin rays 11 to 15, anal fin rays 6 to 9 ..... Antennariidae

4B. Eyes dorsal; dorsal fin spines reduced; mouth small; pectoral fin double, dorsalmost ray of ventral portion membranously attached to side of body; pectoral fin lobe membranously attached to rays of pelvic fin; soft dorsal fin rays 16 or 17, anal fin rays 11 or 12 ..... Tetrabrachiidae

5A. Body slightly compressed laterally; cleft of mouth nearly vertical; frontal bones narrow, meeting each other on the midline along their entire length; lateral ethmoids long and narrow; posteriormost branchiostegal ray free; dorsal fin spines II and III present, embedded beneath skin of head; pelvic fin of one spine and four rays; soft dorsal fin rays 11 to 13; anal fin rays 5 to 7 ..... Chaunacidae

5B. Body strongly depressed dorsoventrally; cleft of mouth horizontal; frontal bones triangular in shape, only their posterior halves meeting on the midline; lateral ethmoids short and stout; posteriormost branchiostegal ray ankylosed to ventromedial margin of subopercle; dorsal fin spine III absent, spine II reduced to a small remnant embedded beneath skin and lying on, or fused to, dorsal surface of pterygiophore just behind base of illicial bone; pelvic fin of one spine and five rays; soft dorsal fin rays 4 or 5; anal fin rays 4 ..... Ogcocephalidae

Although not all of the sister groups suggested are supported by sufficient data at this time, the following classification of the Lophiiformes is proposed. While the ranking of taxa is not dichotomous (see Methods), internested sets of vertical lines are used to indicate sister-group relationships:

Order Lophiiformes
- Suborder Lophioidei
- Suborder Antennarioidei
  - Family Antennariidae
  - Family Tetrabrachiidae
  - Family Lophichthyidae
  - Family Brachionichthyidae
  - Family Chaunacidae
  - Family Ogcocephalidae
- Suborder Ceratioidei

As a final note, the genus *Histionotophorus*, based on a single species, *H. bassani* (Zigno 1887) from the Eocene of Monte Bolca, Italy, should be mentioned. From the available fossil evidence, this genus does not appear to differ substantially from *Brachionichthys*, and probably should be synonymized with the latter (Rosen and Patterson 1969:442). Reconstructions and photographs of the few known specimens (Eastman 1904, text fig. C, pl. 1, fig. 1-3; Gill 1904; Le Danois 1964:141, fig. 75, 76) show the following brachionichthyid features: mouth horizontal; mesopterygoid greatly reduced or absent (?); ectopterygoid absent (?); 22 vertebral

centra; epural absent; dorsal of three well-developed cephalic spines; membrane between dorsal spines II and III (?); caudal fin rays elongate; two elongate pectoral radials.

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LITERATURE CITED

ALLEN, G. R.
1970. Two new species of frogfishes (Antennariidae) from Easter Island. Pac. Sci. 24:517-522.

BEAUFORT, L. F. DE, AND J. C. BRIGGS.
1962. The fishes of the Indo-Australian Archipelago XI. Scleroparei, Hypostomides, Pediculati, Plectognathi, Opisthomi, Discocephali, Xenopterygii. Brill, Leiden, Neth.

BERG, L. S.
1940. Classification of fishes, both recent and fossil. Trav. Zool. Inst. Akad. Nauk SSSR 5:87-517 (reprint, J. W. Edwards, Ann Arbor, Mich., 1947).

BERTELSEN, E.
1951. The ceratioid fishes. Ontogeny, taxonomy, distribution and biology. Dana Rep., Carlsberg Found. 7(39), 276 p.

BOESEMAN, M.
1964. Notes on the fishes of western New Guinea II. *Lophichthys boschmai*, a new genus and species from the Arafoera Sea. Zool. Meded. (Leiden) 39:12-18.

BRADBURY, M. G.
1967. The genera of batfishes (family Ogcocephalidae). Copeia 1967:399-422.

EASTMAN, C. R.
1904. Descriptions of Bolca fishes. Bull. Mus. Comp. Zool. Harv. Coll. 46:1-36.

EATON, T. H., JR., C. A. EDWARDS, M. A. MCINTOSH, AND J. P. ROWLAND.
1954. Structure and relationships of the anglerfish, *Lophius americanus*. J. Elisha Mitchell Sci. Soc. 70: 205-218.

ELDREDGE, N., AND J. CRACRAFT.
1980. Phylogenetic patterns and the evolutionary process. Columbia Univ. Press, N.Y., 349 p.

FIELD, J. G.
1966. Contributions to the functional morphology of fishes. Part II. The feeding mechanism of the anglerfish, *Lophius piscatorius* Linnaeus. Zool. Afr. 2:45-67.

FOWLER, H. W.
1928. The fishes of Oceania. Mem. Bernice P. Bishop Mus. 10, 540 p.

GARMAN, S.
1899. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer "Albatross," during 1891, Lieut. Commander Z. L. Tanner, U.S.N., commanding. XXVI. The fishes. Mem. Harvard Mus. Comp. Zool., Harv. Coll. 24, 431 p.

GILL, T. N.
1882. Supplementary note on the Pediculati. Proc. U.S. Natl. Mus. 5:551-556.
1904. Extinct pediculate and other fishes. Science (Wash., D.C.) 20:845-846.

GREGORY, W. K.
1933. Fish skulls. A study of the evolution of natural mechanisms. Trans. Am. Philos. Soc. 23:75-481.
1951. Evolution emerging. A survey of changing patterns from primeval life to man. Vol. 1, 704 p. Macmillan, N.Y.

GÜNTHER, A.
1880. Report on the shore fishes procured during the voyage of H.M.S. Ch...lenger in the years 1873-1876. Rep. Sci. Res. Voy. Challenger. Zool. 1(6), 82 p.

HENNIG, W.
1966. Phylogenetic systematics. Univ. Ill. Press, Urbana, 263 p.

KAILOLA, P. J., AND M. A. WILSON.
1978. The trawl fisheries of the Gulf of Papua. Papua New Guinea, Dep. Primary Ind., Fish. Res. Bull. 20:1-85.

LE DANOIS, Y.
1964. Étude anatomique et systématique des antennaires, de l'ordre des Pédiculates. Mém. Mus. Natl. Hist. Nat. Paris, Ser. A, Zool. 31:1-162.
1974. Étude ostéo-myologique et révision systématique de la famille des Lophiidae, (Pédiculates Haploptérygiens). Mém. Mus. Natl. Hist. Nat. Paris, Ser. A, Zool. 91, 127 p.
1979. Révision systématique de la famille des Chaunacidae (Pisces Pediculati). UO [Jpn. Soc. Ichthyol.] 30, 76 p.

MONOD, T.
1960. A propos du *pseudobrachium* des *Antennarius* (Pisces, Lophiiformes). Bull. Inst. Fondam. Afr. Noire 22(Ser. A):620-698.

NORMAN, J. R.
1966. A draft synopsis of the orders, families and genera of recent fishes and fish-like vertebrates. Trustees Br. Mus. (Nat. Hist.), Lond., 606 p.

NYBELIN, O.
1963. Zur morphologie und terminologie des Schwanzskelettes der Actinopterygier. Ark. Zool. 15(Ser. 2): 485-516.

PIETSCH, T. W.
1972. A review of the monotypic deep-sea anglerfish family Centrophrynidae: taxonomy, distribution and osteology. Copeia 1972:17-47.
1974. Osteology and relationships of ceratioid anglerfishes of the family Oneirodidae, with a review of the genus *Oneirodes* Lütken. Nat. Hist. Mus. Los Ang. Cty., Sci. Bull. 18:1-113.
1978. A new genus and species of ceratioid anglerfish from the North Pacific Ocean with a review of the allied genera *Ctenochirichthys*, *Chirophryne* and *Leptacanthichthys*. Nat. Hist. Mus. Los Ang. Cty., Contrib. Sci. 297, 25 p.
1979. Systematics and distribution of ceratioid anglerfishes of the family Caulophrynidae with the description of a new genus and species from the Banda Sea. Nat. Hist. Mus. Los Ang. Cty., Contrib. Sci. 310:1-25.
REGAN, C. T.
1903. A revision of the fishes of the family Lophiidae. Ann. Mag. Nat. Hist., Ser. 7, 11:277-285.
1912. The classification of the teleostean fishes of the order Pediculati. Ann. Mag. Nat. Hist., Ser. 8, 9:277-289.
RASQUIN, P.
1958. Ovarian morphology and early embryology of the pediculate fishes *Antennarius* and *Histrio*. Bull. Am. Mus. Nat. Hist. 114:327-371.
ROSEN, D. E., AND C. PATTERSON.
1969. The structure and relationships of the Paracanthopterygian fishes. Bull. Am. Mus. Nat. Hist. 141: 357-474.
SCHULTZ, L. P.
1957. The frogfishes of the family Antennariidae. Proc. U.S. Natl. Mus. 107:47-105.
TAYLOR, W. R.
1967. An enzyme method of clearing and staining small vertebrates. Proc. U.S. Natl. Mus. 122(3596), 17 p.
WHITLEY, G. P.
1934. Abstract of proceedings. Proc. Linn. Soc. N.S.W. 59:xxix-xxxix.
1935. Studies in ichthyology. No. 9. Rec. Aust. Mus. 19:215-250.
WINTERBOTTOM, R.
1974. A descriptive synonymy of the striated muscles of the teleostei. Proc. Acad. Nat. Sci. Phila. 125:225-317.
ZIGNO, A. DE.
1887. Nuove aggiunte alla ittiofauna dell'epoca Eocena. Mem. R. Istit. Veneto 23:31 (not seen).

APPENDIX

The osteological evidence presented in this paper is based on the following list of specimens in addition to the lophiiform material listed in previous studies of the osteology and interrelationships of ceratioid anglerfishes (Pietsch 1972: 44, 1974:109, 1979).

Batrachoididae

Batrachoides pacifici (Günther): MCZ 41805, 153 mm.
Daector dowi (Jordan and Gilbert): LACM 31310-19, 1 (of 3), 97 mm.
Porichthys analis Hubbs and Schultz: LACM 22345, 1 (of 2), 125 mm.
Porichthys notatus Girard: LACM 22083, 1, 114.5 mm.
Porichthys porosissimus (Cuvier and Valenciennes): LACM 30727-11, 1 (of 4), 96 mm.

Lophiidae

Lophius americanus Valenciennes: MCZ 51259, 1, 121 mm.
Lophiodes caulinaris (Garman): MCZ 51260, 1, 33.5 mm.
Lophiodes monodi (Le Danois): MCZ 40928, 1, 92 mm.

Antennariidae

Antennarius avalonis Jordan and Starks: UW 20766, 1, 67 mm.
Antennarius maculatus (Desjardins): UW 20767, 1, 64 mm.
Antennarius sanguineus Gill: LACM 8125, 1 (of 2), 76 mm.
Antennarius striatus (Shaw and Nodder): UW 20768, 2, 65 and 67 mm.
Antennatus bigibbus (Latreille): LACM 32611-1, 1 (of 5), 63 mm.
Echinophryne crassispina McCulloch and Waite: NMV A537, 51 mm.
Histiophryne bougainvilli (Valenciennes): NMV A535, 64 mm.
Histrio histrio (Linnaeus): LACM 8975-1, 1 (of 6), 91 mm.
Histrio histrio (Linnaeus): MCZ 51261, 1, 68 mm.
Rhycherus filamentosus (Castelnau): NMV A536, 56 mm.
Tathicarpus butleri Ogilby: AMS IB.3043, 63 mm.
Trichophryne furcipilis (Cuvier): AMS IA.6631, 50 mm.

Tetrabrachiidae

Tetrabrachium ocellatum Günther: AMS IB.7177, 7188, 2, 56 and 61 mm.

Lophichthyidae

Lophichthys boschmai Boeseman: UW 20773, 2, 44 and 47 mm.

Brachionichthyidae

Brachionichthys hirsutus (Lacepede): AMS IA. 6064, 1, 69 mm.
Brachionichthys hirsutus (Lacepede): UW 20769, 1, 42 mm.
Histionotophorus bassani (Zigno): MCZ 5176A + 5176B, 35 mm; MCZ 5177A + 5177B, 37 mm; MCZ 5178, 33 mm.

Chaunacidae

Chaunax pictus Lowe: UW 20770, 1, 90 mm.

Ogcocephalidae

Dibranchus atlanticus Peters: MCZ 51257, 1, 105 mm.
Zalieutes elater (Jordan and Gilbert): LACM 8824-13, 1 (of 3), 98 mm.

EARLY ZOEAL STAGES OF *LEBBEUS POLARIS*, *EUALUS SUCKLEYI*, *E. FABRICII*, *SPIRONTOCARIS ARCUATA*, *S. OCHOTENSIS*, AND *HEPTACARPUS CAMTSCHATICUS* (CRUSTACEA, DECAPODA, CARIDEA, HIPPOLYTIDAE) AND MORPHOLOGICAL CHARACTERIZATION OF ZOEAE OF *SPIRONTOCARIS* AND RELATED GENERA

EVAN HAYNES[1]

ABSTRACT

Stage I and II zoeae of *Lebbeus polaris*, *Eualus suckleyi*, and *E. fabricii* and Stage I zoeae of *Spirontocaris arcuata*, *S. ochotensis*, and *Heptacarpus camtschaticus* are described from individuals of known parentage. Larval development of *L. polaris* is more abbreviated than larval development of other hippolytid shrimp. Early stage zoeae of *L. polaris* can be distinguished from zoeae of *L. groenlandicus* by differences in morphology of antennal flagellum, maxillipeds, pereopods, and pleopods. Early stage zoeae of *E. suckleyi*, *E. fabricii*, *S. arcuata*, *S. ochotensis*, and *H. camtschaticus* can be distinguished from each other and other known hippolytid zoeae by slight differences in morphology, especially length of rostrum, armature of carapace and abdomen, setation of antennule and mouthparts, and development of pereopods. These new descriptions extend the range of morphological characters of zoeae for each genus and support the proposal that the *Spirontocaris* sensu lato unit be accorded suprageneric status rather than generic status.

Larvae of only a few of the 87 known species of hippolytid shrimp in the northern North Pacific Ocean have been described. Needler (1934) described Stage I zoeae of *Hippolyte clarki* Chace under the name *Hippolyte californiensis* Holmes, and Stage I zoeae of *Eualus herdmani* (Walker), *Heptacarpus brevirostris* (Dana), *H. paludicola* (Holmes), and *H. tridens* (Rathbun) under the generic name *Spirontocaris*. These zoeae were hatched in the laboratory from ovigerous females collected in British Columbia waters. Zoeae and megalopa of *Spirontocaris spinus* (Sowerby) and *S. lilljeborgii* (Danielssen) were described from known parentage and from plankton of eastern Atlantic waters (Pike and Williamson 1961). Pike and Williamson (1961) also described Stage II zoeae of *S. phippsii* (Krøyer) collected from plankton in the western Atlantic and all larval stages of *E. pusiolus* (Krøyer), a species found in the western Atlantic and northern North Pacific Ocean. In addition, Pike and Williamson (1961) described several stages of zoeae presumed to be zoeae of *Lebbeus polaris* (Sabine). Ivanov (1971) described Stage I zoeae of *Eualus macilentus* (Krøyer), *E. barbatus* (Rathbun), *Spirontocaris spinus* (= *S. spina intermedia* Kobjakova), and *Lebbeus groenlandicus* (Fabricius) hatched in the laboratory from ovigerous females collected in the Bering Sea and Gulf of Alaska. Haynes (1978) described the larval stages, including the megalopa, of *L. groenlandicus* from specimens hatched from ovigerous females collected in Kachemak Bay, Alaska.

In this paper, I describe and illustrate zoeal Stages I and II of *L. polaris*, *E. suckleyi* (Stimpson), and *E. fabricii* (Krøyer), and Stage I zoeae of *S. arcuata* (Rathbun), *S. ochotensis* (Brandt), and *H. camtschaticus* (Stimpson) hatched in the laboratory from ovigerous females collected in Kachemak Bay. I also compare the morphology of zoeae of *Spirontocaris* and related genera, and support Pike and Williamson's (1961) proposal to elevate *Spirontocaris* to suprageneric status.

METHODS

From late April to early May 1976, ovigerous *L. polaris*, *E. suckleyi*, *E. fabricii*, *S. arcuata*, *S. ochotensis*, and *H. camtschaticus* were caught in pots at depths of 20-30 m (11-16 fathoms) in Kachemak Bay. The females were transported

[1]Northwest and Alaska Fisheries Center Auke Bay Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 155, Auke Bay, AK 99821.

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to the laboratory and maintained as described by Haynes (1980) for ovigerous *Crangon franciscorum angustimana*. Most zoeae were released at night, about 1 wk after the females were captured. I do not know whether any of the larvae hatched as prezoeae.

For each species, 100 zoeae in groups of 10 zoeae each were placed by large-bore pipette into 500 ml beakers containing about 400 ml of filtered seawater. Seawater in the beakers was changed every other day. Newly hatched nauplii of brine shrimp, *Artemia salina*, from San Francisco Bay were offered, but none were eaten by the zoeae. The zoeae of each species were preserved in 5% Formalin[2] about 10 d after their release. Some of the zoeae of *L. polaris*, *E. suckleyi*, and *E. fabricii* had molted to Stage II.

To study segmentation and setation, I cleared some zoeae in 10% KOH and stained the exoskeleton with Turtox CMC-S (acid fuchsin stain mountant). Because the paired appendages of the zoeae are symmetrical, only the left members are figured. The mandibles, an exception, are drawn as pairs. For clarity in the illustrations, setules on setae are usually omitted, but spinulose setae are shown. Illustrations are partly schematic and represent typical setal counts. Any variation in setal counts is noted in the text.

DESCRIPTION OF ZOEAE

Terms used in the text, nomenclature of gills and appendages, and techniques of measurement and illustration are those given by Haynes (1976). Carapace length refers to the straight-line distance from posterior margin of the orbit to middorsal posterior margin of the carapace. Total body length refers to the distance from the tip of the rostrum to the posterior margin of the telson, not including telsonic spines. Stage I zoeae of *S. ochotensis* lack a rostrum; therefore, for this species only, total body length refers to the distance from anterior middorsal margin of the carapace to posterior margin of the telson. Telsonic setae or spines are numbered from an inner (medial) to outer (lateral) direction. The setation formulas proceed from the distal to the proximal ends of appendages. Principal morphological characteristics used to separate the species of zoeae described in this report are summarized in Table 1.

Lebbeus polaris—Stage I Zoeae

Mean total length of Stage I (Figure 1A), 5.4 mm (range 5.2-5.6 mm, 3 specimens). Rostrum slightly sinuate, without teeth, about one-half length of carapace. Carapace with a rounded prominence at base of rostrum and near posterior margin. Ventral margin of carapace smooth except for pterygostomian spine. No supraorbital spines.

Antennule (Figure 1B).—First antenna, or antennule, an unsegmented peduncle with conical projection and heavily plumose seta. Conical projection with four aesthetascs of various lengths.

Antenna (Figure 1C).—An inner flagellum (endopodite) and outer scale (exopodite). Flagellum two-segmented, slightly longer than scale; distal segment styliform, with terminal plumose seta and short spine. Proximal segment of flagellum has simple seta near joint. Scale distally divided into four joints, fringed with 11 heavily plumose setae. Protopodite with two simple spines: one at base of flagellum, other at base of scale.

Mandibles (Figure 1D).—Well developed, without palps. Four teeth on incisor process of left mandible in contrast to diserrate incisor process

[2]Reference to trade names does not imply endorsement by National Marine Fisheries Service, NOAA.

TABLE 1.—Principal morphological characteristics of hippolytid zoeae described in this report.

Species	Rostrum	Supraorbital spine in Stage I	Abdominal somites bearing posterolateral spines in all stages	Pereopods bearing exopodites	Pereopods in Stage I
Lebbeus polaris	long	no	4, 5	[1]1, 2	5
Eualus suckleyi	long	no	5	[2]1-3	[3]5
E. fabricii	long	no	4, 5	[2]1-3	[3]5
Spirontocaris arcuata	short	no	4, 5	[4]1, 2	[3]5
S. ochotensis	absent	yes	4, 5	[4]1, 2	[3]5
Heptacarpus camtschaticus	minute	no	none	[4]1, 2	[3]5

[1]Small lobe in Stage I and II; absent in later stages.
[2]Poorly developed in Stage I and II; pereopods gradually develop in later stages.
[3]Undeveloped pereopods.
[4]Poorly developed in Stage I; pereopods gradually develop in later stages.

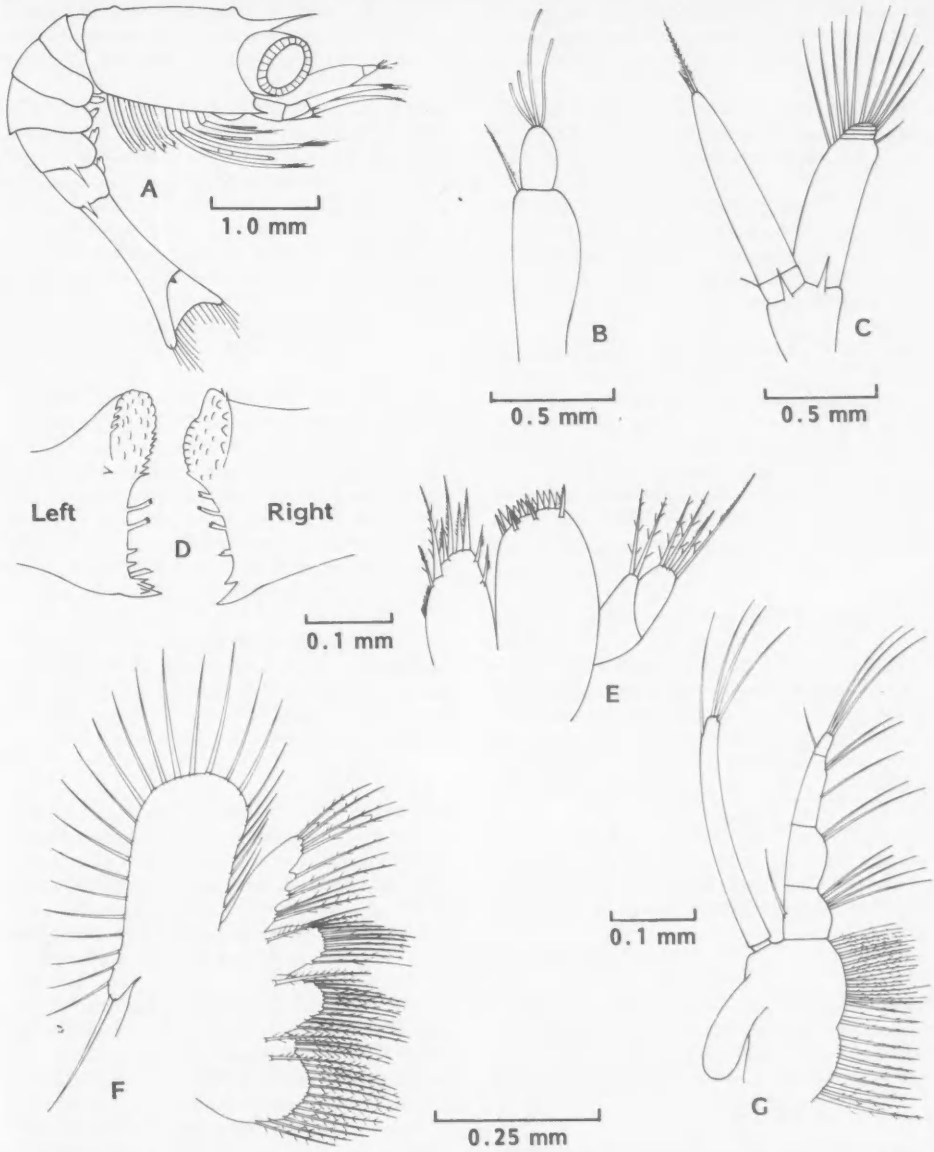

FIGURE 1.—Stage I zoea of *Lebbeus polaris*: A, whole animal, right side; B, antennule, ventral; C, antenna, ventral; D, mandibles, left and right, posterior; E, maxillule, ventral; F, maxilla, dorsal; G, first maxilliped, dorsal.

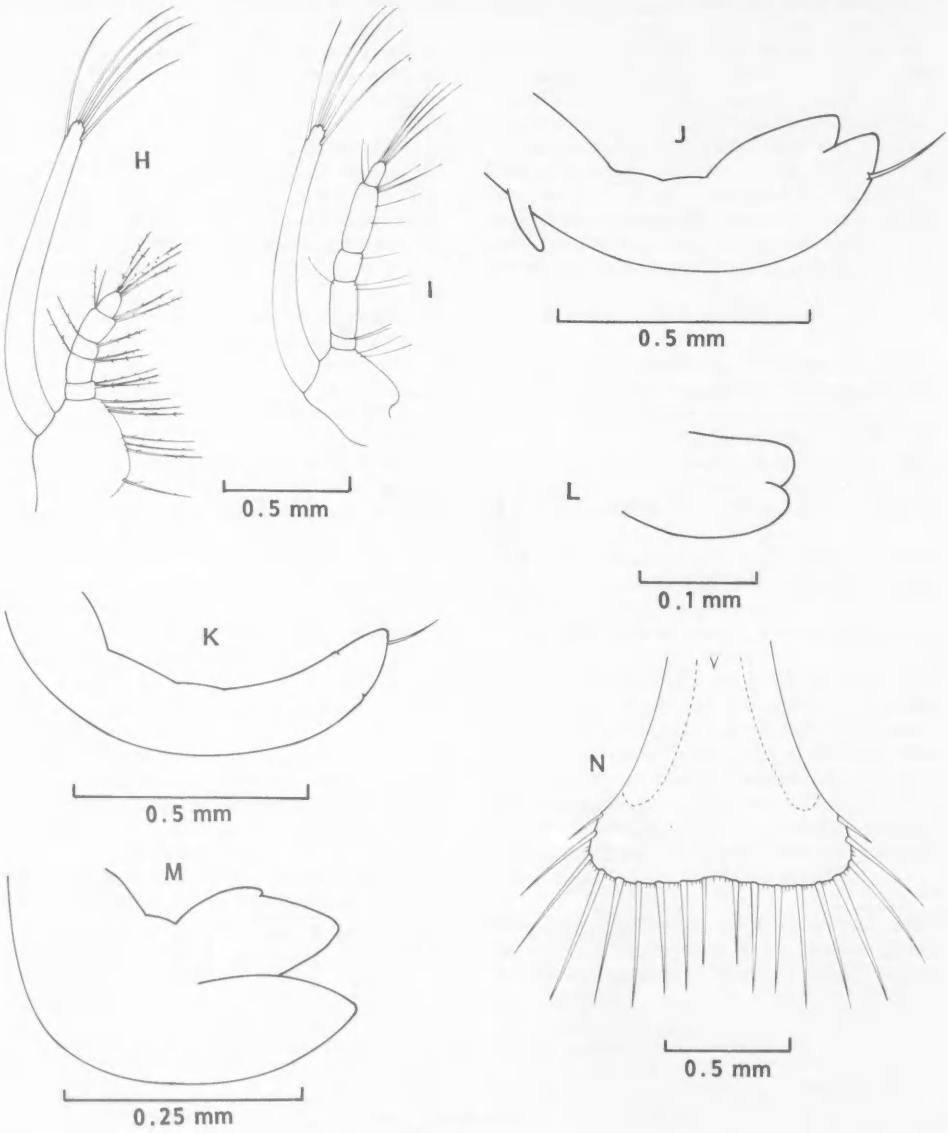

FIGURE 1.—Stage I zoea of *Lebbeus polaris*: H, second maxilliped, dorsal; I, third maxilliped, dorsal; J, first pereopod, right side; K, third pereopod, right side; L, first pleopod, right side; M, second pleopod, right side; N, telson, ventral.

of right mandible. Lacinia mobilis adjacent to incisor process and subterminal tooth on left mandible; neither structure on right mandible.

Maxillule (Figure 1E).—With coxal and basial endites and endopodite on maxillule (first maxilla). Eight setae, all spinulose, on proximal lobe (coxopodite). Fifteen spines terminally (four spines spinulose) on median lobe (basipodite). Two-segmented endopodite on lateral margin of basipodite: distal segment with four, sometimes three, spinulose setae terminally (one seta especially long; remaining three, or two, about equal length); two spinulose setae terminally on proximal segment. No outer seta on maxillule.

Maxilla (Figure 1F).—Platelike exopodite (scaphognathite) with 25 long plumose setae and long thicker seta at proximal end. Both coxopodite and basipodite bilobed. Ten setae on unsegmented endopodite—all setae distinctly setulose. Basipodite with 23 setae: 11 on distal lobe, 12 on proximal lobe. Most, if not all, setae on basipodite and coxopodite setulose. Sixteen setae on coxopodite: 4 on distal lobe, 12 on proximal lobe.

First maxilliped (Figure 1G).—Unsegmented protopodite with 31 spinulose setae: 23 on basipodite, 8 on coxopodite. Endopodite four-segmented; setation formula 4, 3, 2, 6. Exopodite segmented at base, has four natatory setae. Epipodite a single lobe.

Second maxilliped (Figure 1H).—Seven sparsely spinulose setae on unsegmented protopodite. Endopodite five-segmented; fourth segment expanded somewhat laterally; setation formula 5, 4, 2, 3, 3. Exopodite about three times longer than endopodite, not segmented at base. Five natatory setae on exopodite. No epipodite.

Third maxilliped (Figure 1I).—Two simple setae on unsegmented protopodite. Endopodite five-segmented, nearly as long as exopodite; setation formula 5, 5, 1, 3, 2. Setae simple and, except for few terminal setae, minutely spinulose. Exopodite unsegmented at base, has five natatory setae. No epipodite.

First pereopod (Figure 1J).—Endopodite relatively short, wide, unsegmented; chela partially formed; dactylopodite with simple spine. Exopodite, a small lobe.

Second pereopod.—Similar to first pereopod except narrower, exopodite smaller, and chela more deeply cleft.

Third (Figure 1K), *fourth, and fifth pereopods.*—Nearly identical, except size decreases slightly from third to fifth pair. No exopodites.

Pleopods.—First pleopod (Figure 1L) blunt, slightly bilobed. Second pleopod (Figure 1M) bilobed; inner lamella with bud of appendix interna. Third, fourth, and fifth pleopods same as second pleopod. All pleopods without joints or setae.

Abdomen and telson (Figure 1A, N).—Five somites and telson (somite 6 fused with telson). Fourth and fifth abdominal somites with pair of posterolateral spines about half as long as the somites themselves—pair on fifth somite slightly shorter than pair on fourth somite. Telson slightly emarginated distally, has 9 + 9 densely plumose setae; small spinules between bases of all setae except last outer pair of setae. Enclosed uropods visible. Anal spine present but minute.

Lebbeus polaris—Stage II Zoeae

Mean total length of Stage II, 5.7 mm (range 5.6-5.8 mm, 4 specimens). Rostrum (Figure 2A) styliform, not sinuate, without teeth, about one-half length of carapace. Carapace with small supraorbital spine and pterygostomian spine; no spinules along posteroventral margin. Eyes stalked.

Antennule (Figure 2B).—Similar to Stage I antennule, except heavily plumose seta arises from small conical projection. Spine, or seta, and four aesthetascs on tip of large conical projection. Three plumose setae ventrally on distal portion of peduncle.

Antenna (Figure 2C).—Flagellum of antenna three-segmented: terminal segment spined at tip; proximal segment has simple seta. Scale and protopodite similar to scale and protopodite of Stage I.

Mandibles, maxillule, and maxilla.—Nearly identical to Stage I, except molar process of left mandible has several spines along outer margin. Eighteen setae on basipodite of maxillule; 12 setae on coxopodite of maxillule. About 30 setae on scaphognathite of maxilla.

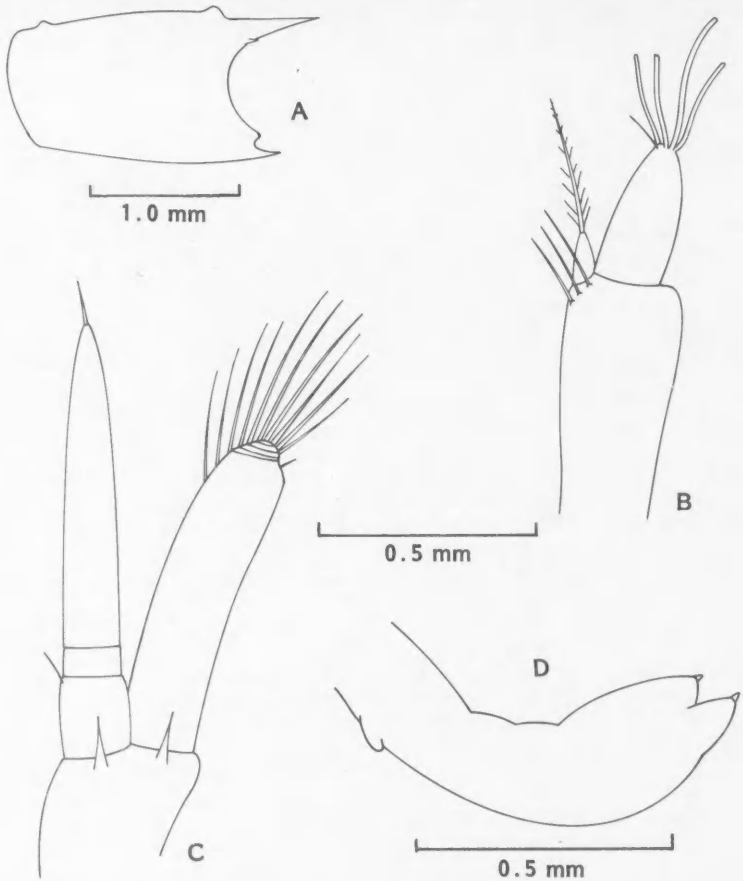

FIGURE 2.—Stage II zoea of *Lebbeus polaris*: A, carapace, right side; B, antennule, ventral; C, antenna, ventral; D, first pereopod, right side.

Maxillipeds.—Same as Stage I.

First pereopod (Figure 2D).—Unsegmented, slightly narrower than in Stage I. Propodite and dactylopodite tipped by small spine; dactylopodite without seta; exopodite remnant.

Second to fifth pereopods.—Similar to Stage I, except second pereopod slightly narrower, without exopodite. Third, fourth, and fifth pereopods with incipient segmentation.

Pleopods.—Similar to Stage I except more bilobed, appendices internae more distinct.

Abdomen and telson.—Nearly identical to Stage I, except sixth abdominal somite and telson jointed. Same number of telsonic setae as in Stage I. Uropods still enclosed.

Eualus suckleyi—Stage I Zoeae

Mean total length of Stage I (Figure 3A), 3.2

mm (range 3.0-3.5 mm, 10 specimens). Rostrum slender, spiniform, without teeth, slightly less than one-half length of carapace. Carapace with small, somewhat angular, dorsomedial prominences at base of rostrum and near posterior edge. Pterygostomian spines present, not hidden by sessile eyes. Several minute spines adjacent to pterygostomian spine: three or four spines on

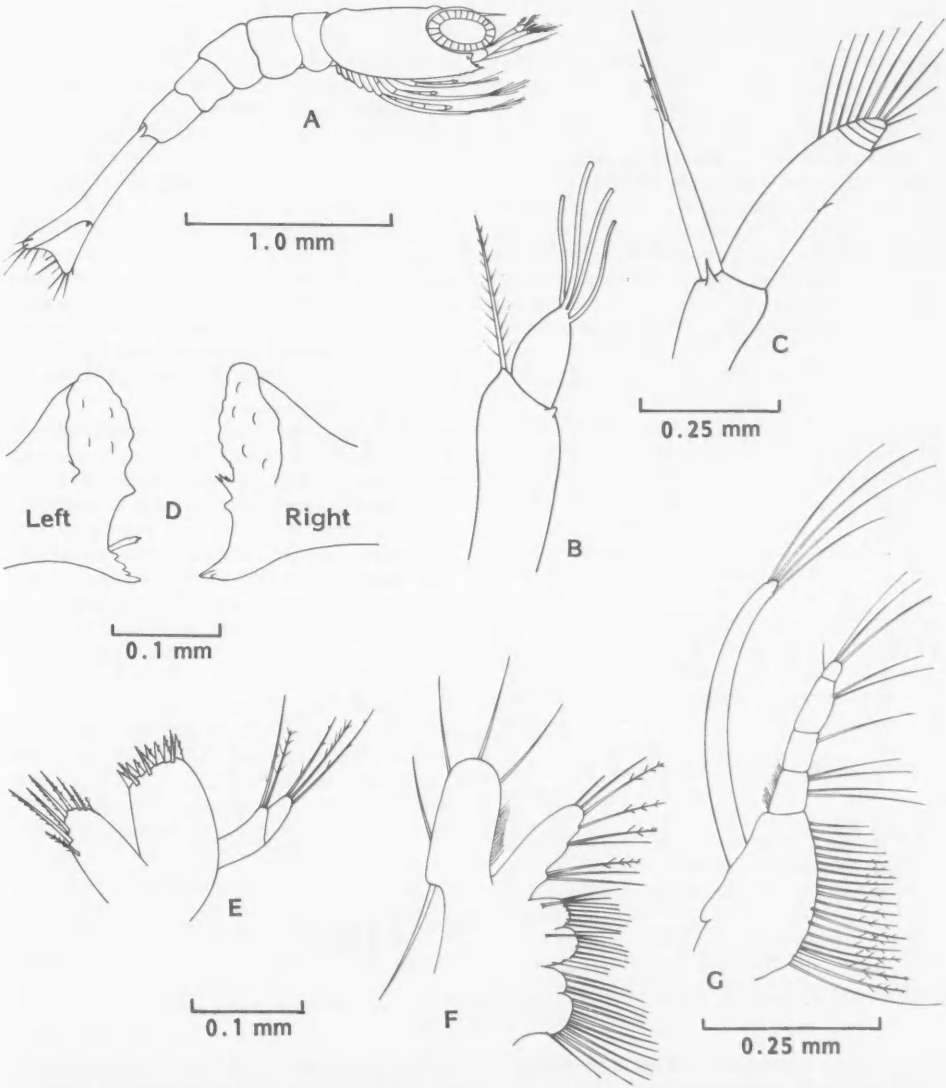

FIGURE 3.—Stage I zoea of *Eualus suckleyi*: A, whole animal, right side; B, antennule, ventral; C, antenna, ventral; D, mandibles, left and right, posterior; E, maxillule, ventral; F, maxilla, dorsal; G, first maxilliped, dorsal.

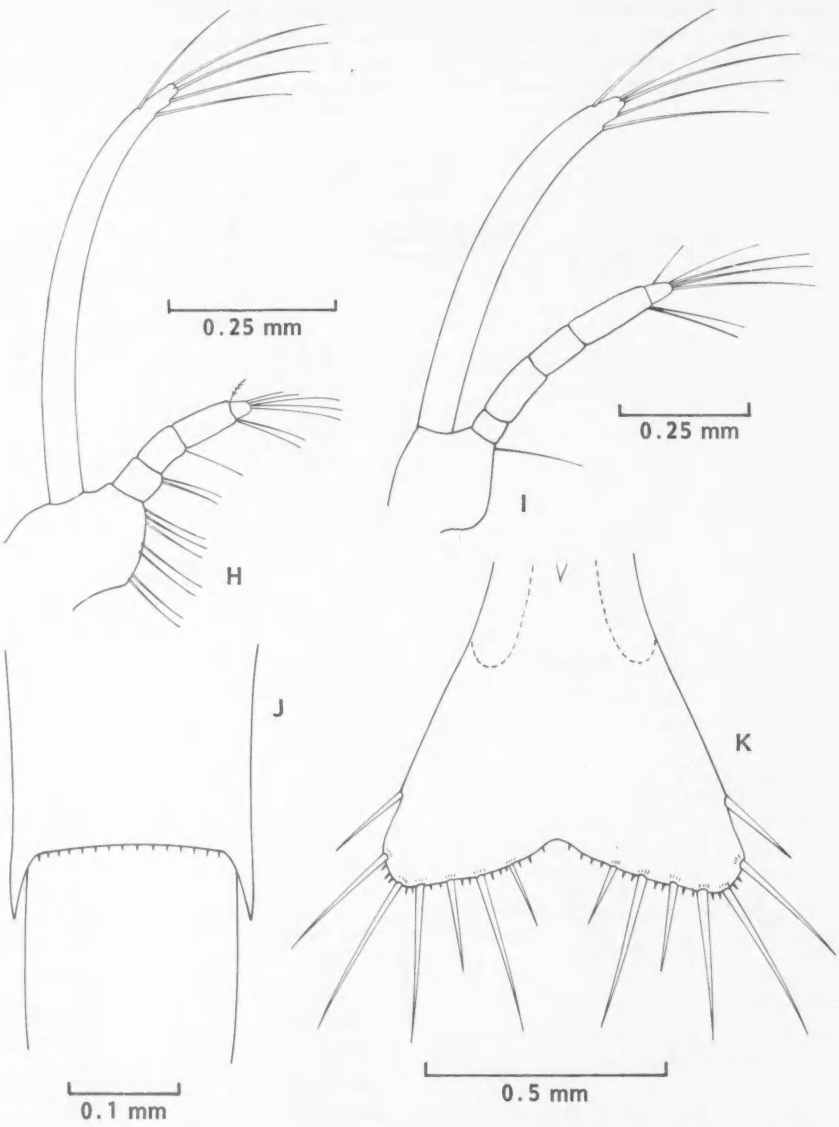

FIGURE 3.—Stage I zoea of *Eualus suckleyi*: H, second maxilliped, dorsal; I, third maxilliped, dorsal; J, fifth abdominal somite, dorsal; K, telson, ventral.

ventral margin of carapace, one spine on anterolateral margin. No supraorbital spines.

Antennule (Figure 3B).—Unsegmented peduncle with conical projection and heavily plumose seta. Four aesthetascs of various lengths on conical projection. Small projection on peduncle near base of conical projection.

Antenna (Figure 3C).—Flagellum unsegmented, shorter and narrower than scale, terminally has plumose seta and shorter spinulose spine. Scale distally divided into four joints, fringed with 11 heavily plumose setae. Small plumose seta about midway on outer lateral margin. Protopodite with spine at base of flagellum but not at base of scale.

Mandibles (Figure 3D).—Well developed, without palps. Incisor process of left mandible with four teeth; incisor process of right mandible triserrate. Left mandible has lacinia mobilis adjacent to incisor process and subterminal tooth on truncated molar process.

Maxillule (Figure 3E).—Coxopodite with eight spinulose setae. Basipodite with 11 spinulose spines terminally. Two-segmented endopodite originating from lateral margin of basipodite has five spinulose setae: three on distal segment, two on proximal segment. Two setae especially spinulose, as shown. No outer seta on maxillule.

Maxilla (Figure 3F).—Scaphognathite with four long plumose setae, slightly longer thicker seta at proximal end, and series of fine hairs along inner margin of exopodite. Unsegmented endopodite with nine setae (four spinulose, as shown). Both basipodite and coxopodite bilobed. Basipodite with 17 setae: 8 on distal lobe, 9 on proximal lobe. Coxopodite with 14 setae: 4 on distal lobe, 10 on proximal lobe. Most, if not all, setae on basipodite and coxopodite setulose.

First maxilliped (Figure 3G).—Unsegmented protopodite with 20 setae; most setae heavily spinulose. Endopodite four-segmented; setation formula 4, 2, 1, 4; series of fine hairs on medial margin of proximal segment. Four natatory setae on exopodite. Epipodite, a small lobe.

Second maxilliped (Figure 3H).—Unsegmented protopodite with seven spinulose setae. Endopodite four-segmented; setation formula 6, 2, 1, 2. Exopodite about three times longer than endopodite, five natatory setae.

Third maxilliped (Figure 3I).—Usually one seta on unsegmented protopodite. Endopodite five-segmented, seven setae: five setae on distal, two on penultimate segment. Exopodite with five natatory setae.

Pereopods.—Poorly developed, unsegmented, and compacted tightly under cephalothorax. Pairs 1-3 biramous, 4 and 5 uniramous.

Pleopods.—Absent.

Abdomen and telson (Figure 3A, J, K).—Five somites and telson (somite 6 fused with telson). Fifth somite with pair of spines on posterolateral margin that extend posteriorly about one-fifth length of fifth somite. Minute spinules along posterodorsal border of fifth somite (Figure 3J) (spinules most easily seen in cleared specimens at ≥100× magnification). Telson (Figure 3K) slightly emarginate distally, bears 7 + 7 densely plumose setae. Third setal pair shorter than second or fourth setal pair. Minute spinules along posterior margin and at base of all setal pairs except possibly outer (seventh) setal pair. Enclosed uropods visible. Anal spine present.

Eualus suckleyi—Stage II Zoeae

Mean total length of Stage II, 3.8 mm (range 3.5-4.2 mm, 8 specimens). Eyes stalked. Rostrum shaped as in Stage I. Carapace with small supraorbital spine, no spinules (Figure 4A).

Antennule.—Similar to Stage I, except peduncle two-segmented with two setae at joint.

Antenna.—Flagellum with terminal spine, no setae, almost same length as scale (Figure 4B). Tip of scale four-segmented, proximal segment incomplete. Scale with 13 plumose setae—no proximal seta near outer lateral margin.

Mandibles, maxillule, and maxilla.—Same as Stage I.

Maxillipeds.—Epipodite of first maxilliped distinctly lobed. Exopodites of maxillipeds 1, 2, and 3 have four, five, and five natatory setae, respectively.

Pereopods.—Poorly developed, tightly compacted under cephalothorax; pairs 1-3 biramous, 4 and 5 uniramous.

Pleopods.—Absent.

Abdomen and telson.—Somite 6 fused with telson. Abdomen retains spines on fifth somite.

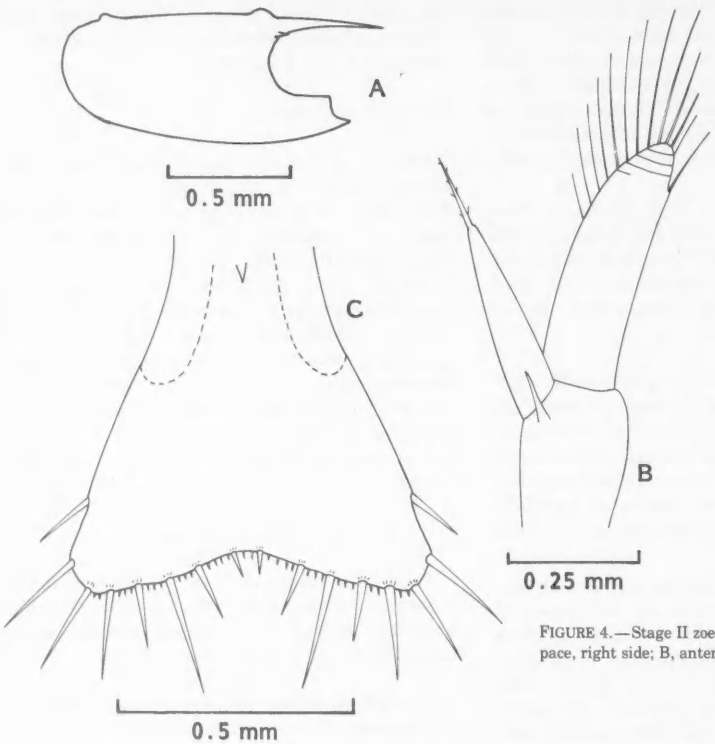

FIGURE 4.—Stage II zoea of *Eualus suckleyi*: A, carapace, right side; B, antenna, ventral; C, telson, ventral.

Telson with 8 + 8 plumose setae; setae noticeably shorter than in Stage I (Figure 4C). Uropods enclosed.

Eualus fabricii—Stage I and II Zoeae

Stage I and II *Eualus fabricii* are similar morphologically to Stage I and II *E. suckleyi*; however, they can be distinguished. Stage I and II of *E. fabricii* are slightly larger than Stage I and II *E. suckleyi*, and armature of the fourth and fifth abdominal somites and numbers of spines and setae differ between the two species.

Stage I Zoeae

Mean total length of Stage I, 3.7 mm (range 3.5-3.8 mm, 10 specimens). Carapace and rostrum similar to those of Stage I *E. suckleyi*, except no spines adjacent to pterygostomian spine on anterior margin of carapace.

Antennule.—Minute projection at base of conical projection of antennule (observable only under high [400×] magnification).

Antenna.—Same as antenna of Stage II *E. suckleyi* (Figure 4B), except flagellum about 1.5 times length of scale.

Mandibles.—Same as Stage I *E. suckleyi.*

Maxillule.—Seven spines on coxopodite; nine spines on basipodite.

Maxilla.—Three (sometimes 4) setae on distal lobe of coxopodite; 11 setae on proximal lobe. Six setae on each lobe of basipodite.

Maxillipeds.—Similar to Stage I *E. suckleyi* except no epipodite on first maxilliped.

Pereopods.—Same as Stage II *E. suckleyi.*

Pleopods.—Absent.

Abdomen and telson.—Pair of lateral spines on fourth and fifth somites. Lateral spines on fourth somite slightly smaller than lateral spines on fifth somite (Figure 5). Minute spinules on posterodorsal margin of fourth and fifth somites: usually one to three on fourth somite, about eight on fifth somite. Minute spinules somewhat variable in size and number, slightly larger than spinules of *E. suckleyi*. Telson same as Stage I telson of *E. suckleyi*.

Stage II Zoeae

Mean total length of Stage II, 4.1 mm (range 4.0-4.3 mm, 10 specimens). Carapace with two spinules immediately posterior to pterygostomian spine; small supraorbital spine present.

Antennule and antenna.—Similar to Stage II *E. suckleyi*, except antennules have only 1 small seta at joint of peduncle and scale with 16 or 17 plumose setae.

Mandibles, maxillule, and maxilla.—Same as Stage I *E. fabricii*.

Maxillipeds.—Exopodites of maxillipeds 1, 2, and 3 have 4, 9, and 10 natatory setae, respectively. Epipodite on first maxilliped undeveloped, not lobed.

FIGURE 5.—Stage I zoea of *Eualus fabricii*: fourth and fifth abdominal somites, right side.

Pereopods.—Pairs 1-3 biramous, 4 and 5 uniramous.

Pleopods.—Absent.

Abdomen and telson.—Fourth and fifth somites with lateral spines, no spinules. Telson fused with sixth somite, has 8 + 8 densely plumose setae. Setae noticeably shorter than in Stage I *E. fabricii*. Uropods enclosed.

Spirontocaris arcuata—Stage I Zoeae

Mean total length of Stage I (Figure 6A), 4.2 mm (range 4.1-4.4 mm, 10 specimens). Rostrum (Figure 6B) spiniform, without teeth, about one-seventh length of carapace, projects downward paralleling contour of eyes. Carapace with small, somewhat angular, dorsal prominence at base of rostrum; another prominence near posterior edge. Pterygostomian spines present, not hidden by sessile eyes. Two or three minute spines along anteroventral margin of carapace. No supraorbital spines.

Antennule (Figure 6C).—Unsegmented peduncle with conical projection and several small simple setae (one seta especially longer than others). Four aesthetascs on small projection on peduncle near base of conical projection.

Antenna (Figure 6D).—Unsegmented flagellum shorter and narrower than scale. Flagellum with spinulose apical spine and several simple setae of various lengths. Scale distally divided into four segments, fringed with 11 heavily plumose setae, has small plumose seta proximally (near outer lateral margin). Protopodite with spine at base of flagellum but not at base of scale.

Mandibles (Figure 6E).—Well developed, without palps. Incisor process of left mandible has four teeth; incisor process of right mandible triserrate. Left mandible with relatively wide lacinia mobilis adjacent to incisor process, subterminal tooth on truncated molar process.

Maxillule.—Maxillule same shape as maxillule of Stage I *E. suckleyi* (Figure 3E). Coxopodite with seven spinulose setae. Basipodite with 10 (sometimes 11) spinulose spines terminally. Endopodite two-segmented, has five spinulose setae: three on

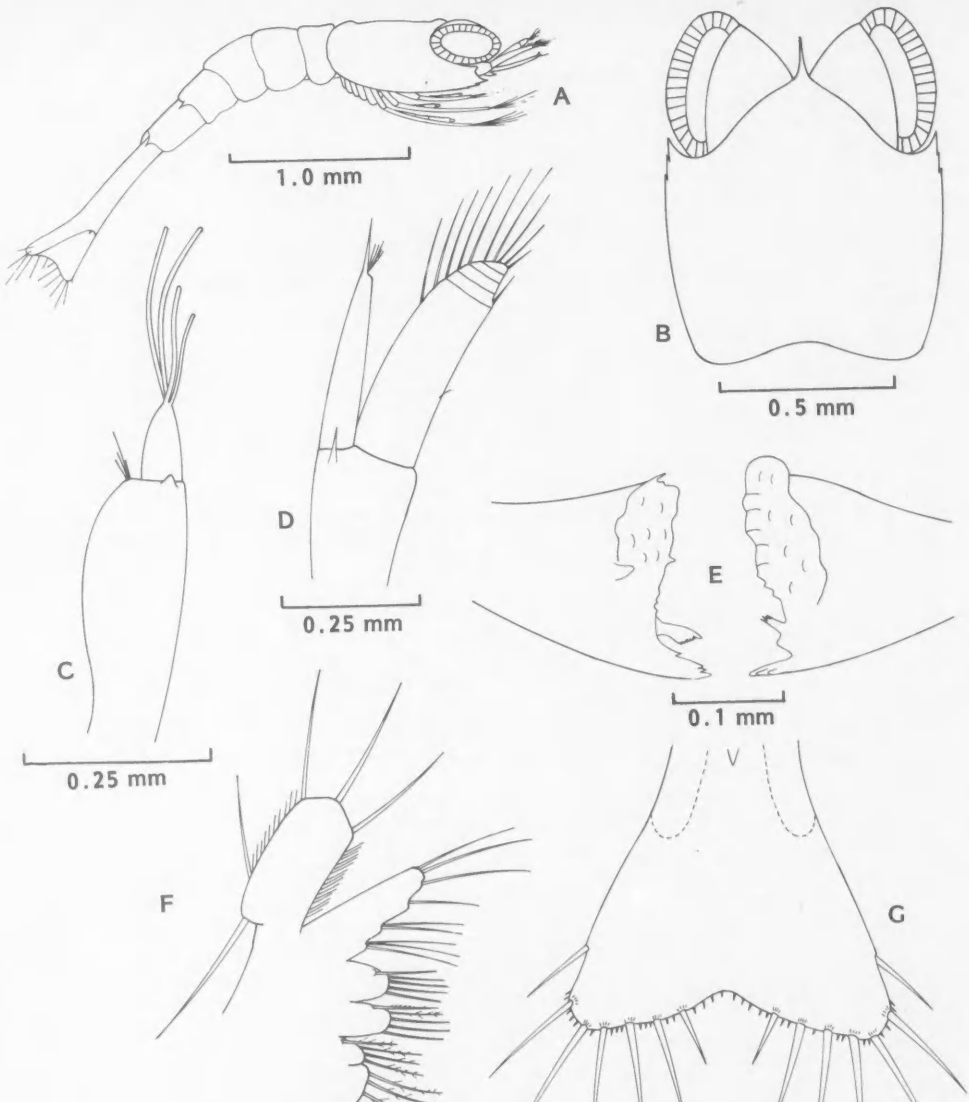

FIGURE 6.—Stage I zoea of *Spirontocaris arcuata*: A, whole animal, right side; B, carapace and eyes, dorsal; C, antennule, ventral; D, antenna, ventral; E, mandibles, left and right, posterior; F, maxilla, dorsal; G, telson, ventral.

distal segment, two on proximal segment. No outer seta on maxillule.

Maxilla (Figure 6F).—Four long plumose setae on scaphognathite; slightly longer, thicker seta at proximal end; series of fine hairs along inner margin; thinner series of hairs along outer margin. Nine setae on unsegmented endopodite. Basipodite and coxopodite bilobed. Basipodite with five setae on each lobe. Coxopodite with 13 setae: 4 on distal lobe, 9 on proximal lobe. Most setae on coxopodite setulose.

First, second, and third maxillipeds.—Maxillipeds similar to Stage I *E. suckleyi*; protopodite of first maxilliped has 25-27 setae; setation formula of endopodite of third maxilliped 5, 2, 1, 1, 4.

Pereopods (Figure 6A).—All five pairs present, poorly developed, unsegmented, and compacted under cephalothorax. Pairs 1 and 2 biramous, 3-5 uniramous.

Pleopods.—Absent.

Abdomen and telson (Figure 6A, G).—Five somites (somite six fused with telson). Fourth and fifth somites with spine but no spinules on posterolateral margins. Telson, shaped as in Stage I *E. suckleyi* (Figure 3K), has 7 + 7 densely plumose setae. Second and third pair of telsonic setae are same length. Minute spinules along terminal margin and at base of each seta except possibly last setal pair. Enclosed uropods visible. Anal spine present.

Spirontocaris ochotensis— Stage I Zoeae

Stage I *S. ochotensis* similar to Stage I *S. arcuata*. *Spirontocaris ochotensis* smaller than *S. arcuata* and lacks rostrum; morphology of carapace, antenna, mandibles, and maxilla slightly different. Characters not mentioned are identical to Stage I *S. arcuata*.

Mean total length of Stage I, 2.8 mm (range 2.7-2.9 mm, 10 specimens). Carapace of *S. ochotensis* without rostrum. Pterygostomian spine and usually a spine along anteroventral margin of carapace (Figure 7A). Minute supraorbital spines present.

Antenna.—Plumose seta three times length of terminal spine on tip of flagellum (Figure 7B).

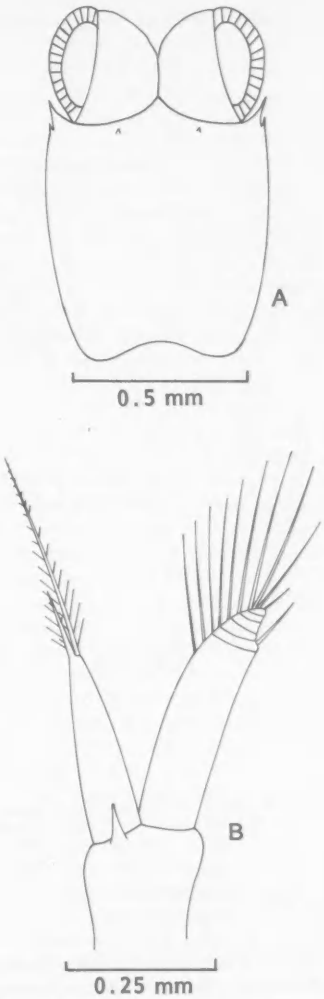

FIGURE 7.—Stage I zoea of *Spirontocaris ochotensis*: A, carapace and eyes, dorsal; B, antenna, ventral.

Mandible.—Narrow lacinia mobilis on left mandible (as in Stage I *E. suckleyi*, see Figure 3D).

Maxilla.—Seven (rarely eight) plumose setae on exopodite.

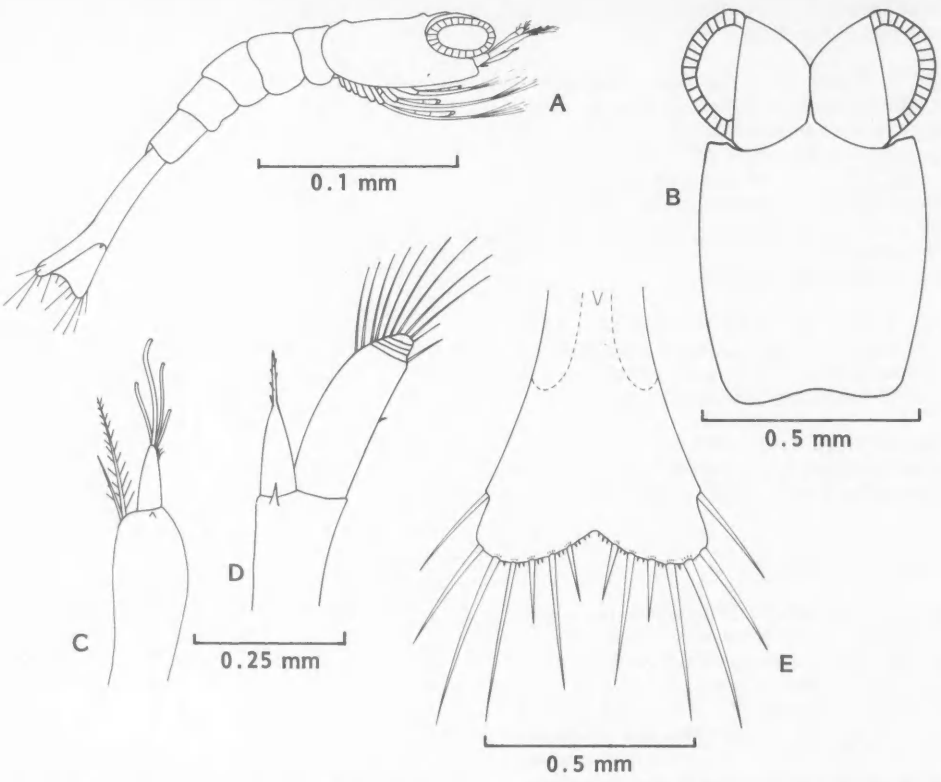

FIGURE 8.—Stage I zoea of *Heptacarpus camtschaticus*: A, whole animal, right side; B, carapace and eyes, dorsal; C, antennule, ventral; D, antenna, ventral; E, telson, ventral.

Heptacarpus camtschaticus— Stage I Zoeae

Mean total length of Stage I (Figure 8A), 2.9 mm (range 2.8-3.1 mm, 10 specimens). Carapace without spines; minute rostrum curves slightly downward following dorsal contour of sessile eyes (Figure 8B).

Antennule (Figure 8C).—Unsegmented peduncle with conical projection, plumose seta, simple spine, and small projection. Plumose seta about twice length of conical projection. Conical projection has four aesthetascs terminally, three small aesthetascs subterminally.

Antenna (Figure 8D).—Unsegmented flagellum about three-fourths length of scale, tipped by stout spinulose spine. Scale similar to scale of Stage I *E. suckleyi* (Figure 3C) except noticeably shorter and wider.

Mandibles, maxillule, maxilla, and maxillipeds.—Mouthparts similar to those of Stage I *E. suckleyi*, except coxopodite of maxillule has seven spinulose setae; basipodite of maxilla has six setae on each lobe; first maxilliped has no epipodite; setation formulas of the endopodites of the second and third maxillipeds are 5, 2, 1, 3 and 4, 2, 0, 0, 2, respectively.

Pereopods (Figure 8A).—All five pairs present: pairs 1 and 2 biramous; 3-5 uniramous.

Pleopods.—Absent.

Abdomen and telson (Figure 8A, E).—Abdomen similar in shape to abdomen of Stage I *E. suckleyi* except without spines or spinules. Telson emarginated, bears 7 + 7 relatively long densely plumose setae: longest (fifth) pair about three-fourths length of greatest telsonic width. Minute spinules along terminal margin of telson and at base of each seta to fifth setal pair. Anal spine present.

COMPARISON OF ZOEAL STAGES WITH DESCRIPTIONS BY OTHER AUTHORS

In the literature, authors have identified or assigned names or stages to hippolytid larvae obtained from plankton. A comparison of their descriptions with my descriptions of zoeae of known parentage is useful in placing these earlier works in proper perspective (Table 2).

TABLE 2.—Presumed and corrected identities of hippolytid zoeae discussed in this report.

Author	Presumed identity	Conclusion from this study
Stephensen (1916)	*S. polaris* (= *L. polaris*) Stage I	Probably *L. polaris* Stage III or later
	Spirontocaris-larva Nr. 3	Not *E. fabricii*
	S. fabricii (= *E. fabricii*)	
	"youngest" stage (Stage I)	Stage III
	"intermediate" stage (Stage II)	Stage IV
	"oldest" ("last") stage (Stage III)	Stage V or VI
Stephensen (1935)	*Spirontocaris*-larva No. 1	Unknown
	S. polaris (= *L. polaris*) Stages not specified	—
Frost (1936)	*E. fabricii* Late-stage larvae	Not *E. fabricii* Stage VI or VII
Makarov (1967)	*Lebbeus* sp. "C" Stage II	*Lebbeus* sp. Stage I
	Lebbeus sp. "D"	*Lebbeus* sp.; different species from *Lebbeus* sp. "C"
	Stage I	Stage I
	"*Eualus* sp. A" *E. fabricii* Stage I	Not *E. fabricii* Stage I
	"*Spirontocaris* sp. A" *S. phippsii* Stage I	Not *S. arcuata* Stage I
	"*Spirontocaris* sp. B" Stage I	Not *S. arcuata* Stage I

Lebbeus polaris

Krøyer (1842, in Pike and Williamson 1961) described an advanced embryo of *L. polaris* with all appendages, except uropods, present and segmented. The fourth and fifth abdominal somites each have a pair of small posterolateral spines. All three pairs of maxillipeds have natatory exopodites, but the pereopods have none. As far as can be compared, my Stage I zoeae of *L. polaris* are identical to Krøyer's embryo, except the pereopods and pleopods of my specimens are unsegmented.

Stephensen, in 1916, described a zoea from southern waters of Greenland that he assumed is a Stage I zoea of *S. polaris* (= *L. polaris*). As noted by Pike and Williamson (1961), Stephensen's zoea is similar to Krøyer's specimen. Stephensen's zoea has posterolateral spines on the fourth and fifth abdominal somites, lacks exopodites on the pereopods, and the appendages are larger and more developed than Krøyer's specimen. The carapace of Stephensen's zoea has supraorbital spines, and developing uropods are visible inside the telson. In addition, the chelae of the first and second pereopods of Stephensen's zoea are well developed; the carpopodite of the second pereopod had begun to develop joints; and the pleopods have well-developed appendices internae. The presence of appendices internae, well-developed chelae, and segmentation of carpopodite shows that Stephensen's zoea is in the last, or perhaps penultimate, zoeal stage and that the species passes through only three or, perhaps, four zoeal stages. Under the name "*Spirontocaris*-larva No. 1," Stephensen (1935) included several specimens collected from waters of western Greenland that he assumes are later stages of *S. polaris* (= *L. polaris*); one specimen bears exopodites on pereopods 1 and 2.

The characteristics of Stephensen's (1916) late-stage "*S. polaris*" zoea are typical of *Lebbeus* zoeae although his zoea differs somewhat from my *L. polaris* zoeae. Stephensen's zoea has an unsegmented antennal flagellum, and the telson is fused with the sixth somite; my zoeae of *L. polaris* have a two-segmented antennal flagellum in Stage I, and the sixth somite and telson are jointed in Stage II. If Stephensen was correct in assuming his specimen to be *L. polaris*, then *L. polaris* in Greenland waters has at least one more zoeal stage than *L. polaris* in Alaskan waters. Stephensen's (1935) descriptions of his "*Spirontocaris*-larva No. 1" zoeae are too brief to identify either the species or stage. At least one of Stephensen's specimens lacks the pair of spines on the antennal protopodite and must be a species other than *L. polaris*.

Makarov (1967) briefly described zoeae collected from plankton of the western Kamchatka Peninsula shelf. He thought these zoeae were probably

zoeal Stages I-IV of a species of *Lebbeus*. He also obtained one specimen each of "*Lebbeus* sp. D" and "*Lebbeus* sp. C"; these he thought were zoeal Stages I and II, respectively. My Stage I zoeae of *L. polaris* are similar to Makarov's Stage I zoea ("*Lebbeus* sp. D") except my zoeae are not as long (average length 5.4 mm compared with 6.4 mm). Makarov's Stage II zoea ("*Lebbeus* sp. C") is 7.6 mm long; the eyes are sessile; and the carapace lacks supraorbital spines. My Stage II zoeae of *L. polaris* are 5.7 mm (mean) long; the eyes are stalked; and the carapace has supraorbital spines. Development of Makarov's "*Lebbeus* sp. C" and "*Lebbeus* sp. D" zoeae shows that they are undoubtedly zoeae of the genus *Lebbeus*. Because his "*Lebbeus* sp. C" zoea has sessile eyes and does not have supraorbital spines, it must be a Stage I zoea rather than a Stage II zoea. "*Lebbeus* sp. C," therefore, is a species different from "*Lebbeus* sp. D."

Larvae of only one other species of *Lebbeus*, *L. groenlandicus*, have been completely described from known parentage (see Haynes 1978). At comparable zoeal stages, *L. groenlandicus* is more developed than *L. polaris*. The antennal flagellum of Stage I zoeae of *L. groenlandicus* is about twice as long as the scale and terminates in a narrow projection. In *L. polaris*, the antennal flagellum is only slightly longer than the scale and has a plumose seta and spine. Also, in Stage I zoeae of *L. groenlandicus*, the epipodite of the first maxilliped is bilobed; the second maxilliped has a single lobed epipodite; and pereopods and pleopods are either partially or fully segmented. In *L. polaris*, only the first maxilliped bears an epipodite (single lobed), and none of the pereopods or pleopods are either partially or fully segmented.

In Stage II zoeae of *L. groenlandicus*, the supraorbital spine is well developed; the antennule differs considerably from the antennule of Stage I; the antennal flagellum has setae; the antennal scale is fringed with plumose setae along nearly the entire inner margin; the pereopods are essentially adult in shape; and the pleopods are fully segmented. In Stage II *L. polaris*, the supraorbital spine is small; the antennule and antennae are similar to the antennule and antennae of Stage I; the pereopods are not adult in shape; and the pleopods are unsegmented.

Lebbeus groenlandicus has only three larval stages: two zoeal stages and one megalopal stage (Haynes 1978). Because larvae of *L. polaris* are somewhat less developed for a given stage than those of *L. groenlandicus*, *L. polaris* probably has three zoeal stages before molting to the megalopa.

Eualus suckleyi

Zoeal Stages I and II of *E. suckleyi* are similar to the same zoeal stages of *E. gaimardii* (H. Milne Edwards), *S. spinus*, and *S. lilljeborgii* (as Pike and Williamson [1961] described them from eastern Atlantic specimens); however, there are slight differences in setation, development of pereopods, and armature of carapace and abdomen. The antennal flagellum of Stage I zoeae of *E. suckleyi* has a spine and a seta; the antennal scale has a plumose seta at the base of each of the four segments; and pereopods 1-5 are present (pereopods 1-3 biramous, other pereopods uniramous). The antennal flagellum of Stage I zoeae of *E. gaimardii* has only a spine; the antennal scale has a small outer spine at the base of the four segments; and pereopods 1-4 are present and uniramous. Stage I zoeae of *S. spinus* and *S. lilljeborgii* lack minute spines on the anteroventral margin of the carapace, have a rudimentary supraorbital spine, and only pereopods 1 and 2 are biramous. Also, *S. spinus* has posterolateral spines on abdominal somites 4 and 5 rather than only on somite 5 as in *E. suckleyi*.

In Stage II zoeae of *E. suckleyi*, an outer plumose seta is at the base of the distal joints of the antennal scale; and exopodites on maxillipeds 1-3 have four, five, and five natatory setae, respectively. In Stage II zoeae of *E. gaimardii*, a somewhat stout spine is at the base of the distal joints of the antennal scale, and exopodites on maxillipeds 1-3 have five, seven, and seven natatory setae, respectively. Stage II zoeae of both *S. spinus* and *S. lilljeborgii* have a tuft of dorsal setae on abdominal somite 4; Stage II zoeae of *E. suckleyi* do not have this tuft.

Eualus fabricii

Stephensen's (1916) "*Spirontocaris*-larva Nr. 3" were the most abundant spirontocarid larvae in his plankton samples from Greenland waters. He thought the larvae were the same species as the most abundant adult and described and illustrated them as the "youngest" stage, "intermediate" stage, and "oldest" ("last") stage of *Spirontocaris fabricii* (= *Eualus fabricii*). Stephensen (1935) later described additional characteristics for the "first" and "last" stages. Frost

(1936) illustrated a whole zoea she believed was a zoeal stage of *E. fabricii* later than Stephensen's "last" stage. Pike and Williamson (1961), from development of zoeae of the genus *Eualus*, showed that Stephensen's "youngest" stage is Stage III; the "intermediate" stage is Stage IV; and the "oldest" stage is Stage V or VI. They believed that the zoea illustrated by Frost (1936) is probably Stage VI or VII.

Although Stephensen's and Frost's *E. fabricii* zoeae are later stages than my zoeae, they can be compared with my zoeae by the presence of posterolateral spines on abdominal somites, length of the antennal flagellum, and number of setae fringing the antennal scale. My *E. fabricii* zoeae have posterolateral spines on abdominal somites 4 and 5; Stephensen's and Frost's zoeae do not. The antennal flagellum in Stages I and II of my *E. fabricii* zoeae is about 1.5 times the length of the antennal scale, and the antennal scale has 13 setae in Stage I and 16 or 17 setae in Stage II. In the "youngest" stage (Stage III zoeae) described by Stephensen, the length of the antennal flagellum is still only about one-half the length of the antennal scale, and the number of setae on the antennal scale does not exceed 11. Stephensen's and Frost's zoeae apparently belong to a species other than *E. fabricii*.

Pike and Williamson (1961) noted that the zoeae described by Stephensen (1916, 1935) and Frost (1936) as *S. fabricii* (= *E. fabricii*) are similar to zoeae of *E. pusiolus*. The zoeae of both species lack abdominal spines and have exopodites on pereopods 1-4. However, *E. fabricii* zoeae are larger, have a longer rostrum, and have a well-developed antennal spine on the anterior margin of the carapace in late zoeal stages (compared with *E. pusiolus* zoeae). On the basis of Pike and Williamson's comparison of zoeae of *E. fabricii* and *E. pusiolus*, Makarov (1967) suggested that his "*Eualus* sp. A" series of zoeae from the west Kamchatka shelf is either *E. pusiolus* or *E. fabricii*. According to Makarov, "*Eualus* sp. A" zoeae are nearly identical to zoeae of *E. pusiolus* described by Pike and Williamson (1961), but because Makarov's zoeae are larger, especially in the later stages, he speculated that "*Eualus* sp. A" zoeae might be *E. fabricii* zoeae.

Stage I and II zoeae of Makarov's "*Eualus* sp. A" differ considerably from my Stage I and II zoeae of *E. fabricii*. The zoeae of "*Eualus* sp. A" are markedly smaller (Stages I and II of "*Eualus* sp. A" are 2.8 mm and 3.2 mm long, respectively; Stage I and II *E. fabricii* are 3.7 mm and 4.1 mm long, respectively). The rostrum of Makarov's zoeae is minute; the abdomen lacks spines; and the antennal flagellum is noticeably shorter than the antennal flagellum of my Stage I and II *E. fabricii*.

Spirontocaris arcuata

Pike and Williamson (1961) described a Stage I zoeae of *S. spinus* and *S. lilljeborgii* hatched from known parentage and a Stage II zoea of *S. phippsii* collected from plankton. My Stage I zoeae of *S. arcuata* are clearly different from these zoeae. Stage I zoeae of *S. arcuata* differ from those of *S. spinus* and *S. lilljeborgii* in shape of rostrum, armature of carapace and abdomen, and setation of antennule and antennae. Stage I *S. arcuata* zoeae have a short rostrum that does not project beyond the anterior margin of the eyes. In Stage I zoeae of *S. spinus* and *S. lilljeborgii* and Stage II zoeae of *S. phippsii*, a prominent rostrum projects anteriorly beyond the eyes to about three-fourths the length of the antennular peduncle. The carapace of my specimens of *S. arcuata* does not have supraorbital spines but has spines along the anteroventral margin. However, in Stage I *S. spinus* and *S. lilljeborgii* and Stage II *S. phippsii*, the carapace has a small supraorbital spine, and the anteroventral margin is smooth. Also, in Stage I zoeae of *S. arcuata*, the antennule and inner flagellum of the antenna have several setae terminally. Both the antennule and inner antennal flagellum of Stage I zoeae of *S. spinus* and *S. lilljeborgii* and Stage II zoeae of *S. phippsii* have a large seta terminally. Finally, Stage I zoeae of *S. lilljeborgii* have posterolateral spines only on the fourth abdominal somite; Stage I zoeae of *S. arcuata* have posterolateral spines on both fourth and fifth abdominal somites.

Makarov (1967) described Stage I zoeae of two unidentified species of *Spirontocaris* ("species A" and "species B") from plankton of the western Kamchatka Peninsula shelf. His zoeae can be separated from Stage I zoeae of *S. arcuata* by the relatively long rostrum in his species A and B. In addition, Makarov's Stage I zoeae of *Spirontocaris* sp. B are longer than those of *S. arcuata* (5.1 mm and 4.2 mm, respectively) and have pleopodal buds.

Ivanov (1971) briefly described four zoeae he assumed were *S. spina intermedia*. His zoeae are readily distinguishable from zoeae of *S. arcuata*

because *S. spina intermedia* has a tuft of setae on the dorsal surface of the fourth abdominal somite.

Spirontocaris ochotensis

When descriptions of hippolytid zoeae by other authors (Stephensen 1916, 1935; Webb 1921; Lebour 1931, 1932; Needler 1934; Frost 1936; Gurney 1942; Williamson 1957; Pike and Williamson 1961; Makarov 1967; Ivanov 1971; and Haynes 1978) are compared with my description of zoeae of *S. ochotensis*, my Stage I zoeae of *S. ochotensis* are the only described hippolytid zoeae of the northern North Pacific Ocean that have posterolateral spines on the fourth and fifth abdominal somites and lack a rostrum. Stage I zoeae of *S. arcuata* (described in this report) are similar to Stage I *S. ochotensis* zoeae but have a rostrum.

Heptacarpus camtschaticus

The only larvae of *Heptacarpus* identified are the first zoeal stages of three species that Needler (1934) described: *H. paludicola*, *H. tridens*, and *H. brevirostris*. These zoeae differ from *H. camtschaticus*: Needler's zoeae lack a rostrum, a spine adjacent to the plumose seta of the antennule, and a long proximal seta on the scaphognathite of the maxilla. Also, Needler's zoeae have pterygostomian spines, which are absent in Stage I zoeae of *H. camtschaticus*.

Stage I zoeae that resemble Stage I zoeae of *H. camtschaticus* include *E. pusiolus* and *E. occultus* found in European waters (Pike and Williamson 1961) and *E. macilentus* found in the Bering Sea (Ivanov 1971). All these Stage I zoeae lack posterolateral spines on the fourth and fifth abdominal somites and have a minute rostrum (although Stage I zoeae of *E. occultus* from British waters may lack a rostrum [Pike and Williamson 1961]). Stage I zoeae of *H. camtschaticus* differ from the other Stage I zoeae because *H. camtschaticus* zoeae have all pairs of pereopods, and the antennal flagellum projects only about three-fourths the length of the antennal scale. In Stage I, the other species lack pereopods, and the antennal flagellum projects to the tip of the antennal scale or just beyond. In addition, Stage I zoeae of *E. occultus* have a small dorsal tuft of setae on the fourth abdominal somite and a row of fine denticles on the posterior margin of the fifth abdominal somite; these structures are absent in Stage I zoeae of *H. camtschaticus*.

CHARACTERIZATION OF ZOEAE OF *SPIRONTOCARIS* S.S. AND RELATED GENERA

Holthuis (1947) redefined the genus *Spirontocaris* sensu lato (s.l.) and divided it into six genera: *Birulia*, *Eualus*, *Heptacarpus*, *Lebbeus*, *Spirontocaris* sensu stricto (s.s.), and *Thoralus*. Pike and Williamson (1961) categorized the zoeae of *Spirontocaris* s.l. by the number of zoeal stages, number of pereopods, morphology of the rostrum in Stage I, and number of pereopods with exopodites in the last zoeal stage. Because of the wide range in morphology of the zoeae, Pike and Williamson (1961) suggested that *Spirontocaris* s.l. be given suprageneric status. My descriptions of hippolytid zoeae partially invalidate Pike and Williamson's categorization, extend the range of larval characters of the genus *Spirontocaris* s.l., and confirm Pike and Williamson's suggestion that *Spirontocaris* s.l. be given suprageneric status.

In Pike and Williamson's (1961) categorization, the known larvae of *Lebbeus* and *Spirontocaris* s.s. form separate generic groups. They categorize identified larvae of *Eualus* spp. into two distinct groups. Group 1 includes *E. gaimardii*, which has five zoeal stages. In Stage I zoeae of Group 1, the rostrum is large, and four pairs of undeveloped pereopods are present; in later zoeal stages, exopodites are present on pereopods one through three. Group 2 includes *E. pusiolus*, *E. occultus*, *E. fabricii*, and *E. herdmani*, which probably have six to nine zoeal stages. In Stage I zoeae of Group 2, the rostrum is minute or absent, and there are no pereopods. In later zoeae, exopodites are present on pereopods one through four (evidence was incomplete for *E. fabricii* and *E. herdmani*). The lack of information on larvae of *Heptacarpus* spp. prevents any comparison of *Heptacarpus* spp. larvae to those of Group 2 *Eualus*.

My descriptions of zoeae of *L. polaris*, *E. suckleyi*, *E. fabricii*, *S. arcuata*, *S. ochotensis*, and *H. camtschaticus* increase the range of morphological variations of zoeal "generic" characters used by Pike and Williamson (1961) for these genera (Table 3). Pike and Williamson list the rostrum of *Lebbeus* spp. zoeae in Stage I as small, but the rostrum may also be large (about one-half the length of the carapace). They list the rostrum in Stage I zoeae of *Spirontocaris* s.s. as large, but the rostrum of Stage I zoeae of *S. arcuata* is small (about one-seventh the length of the carapace), and the rostrum of Stage I zoeae of *S.*

TABLE 3.—Range of morphological and developmental characters used to define zoeae of *Spirontocaris* s.s. and related genera. (? = unknown.)

Genus	Characters				
	Number of zoeal stages	Number of pereopods in Stage I	Rostrum in Stage I	Pereopods bearing exopodites in later zoeal stages	References[1]
Lebbeus sp.	2, 3	5	long	0	1, 2, 3
Eualus sp.	5-9	0, [2]4, [2]5	absent to long	3, 4	1, 3, 4, 5, 6, 7
Spirontocaris s.s.	5	[2]5	absent to long	2	1, 3, 4, 6, 8
Heptacarpus sp.	?	0, [2]5	absent, minute	?	1, 5
Thoralus sp.	9	0	absent, minute	3	4, 9, 10

[1]1) Haynes 1978, 2) this report, 3) Ivanov 1971, 4) Pike and Williamson 1961, 5) Needler 1934, 6) Williamson 1957, 7) Lebour 1940, 8) Lebour 1937, 9) Lebour 1932, 10) Lebour 1936.
[2]Undeveloped pereopods.

ochotensis is absent. Stage I zoeae of both *E. suckleyi* and *E. fabricii* have large rostrums (about one-half the length of the carapace) and, therefore, correspond to Pike and Williamson's *Eualus* Group 1 but also have some of the characters of Group 2. Additionally, zoeae of *E. suckleyi* and *E. fabricii* have five pairs of undeveloped pereopods rather than four pairs of undeveloped pereopods like Stage I zoeae of *E. gaimardii*. The genus *Heptacarpus* is characterized by Pike and Williamson (1961) by the absence of both rostrum and pereopods in Stage I, but Stage I zoeae of *H. camtschaticus* have both a minute rostrum and all five pairs of undeveloped pereopods.

Although my new descriptions of zoeae extend the range of morphological characters of the genus *Spirontocaris* s.l. and partially invalidate the generic groupings used by Pike and Williamson (1961), these new descriptions confirm their findings of great morphological variation of the zoeae of *Spirontocaris* s.l. The range of two to nine zoeal stages among the species is unequalled in any described genus. Usually Stage I zoeae of a caridean genus vary little in the degree of development at hatching, but *Spirontocaris* s.l. includes some species that have Stage I zoeae with all appendages, except uropods, present and segmented and other species of Stage I zoeae that have no trace of appendages posterior to the maxillipeds. The size of the zoeal rostrum is frequently of generic importance. Among species of the spirontocarid group, the rostrum varies from being absent to large. Also, the number of pereopods with exopodites in later zoeal stages is constant throughout known zoeae of nearly all caridean genera except *Spirontocaris* s.l., which may have 0, 2, 3, or 4 pereopods (Pike and Williamson 1961). The wide range in morphology of different species in the *Spirontocaris* s.l. supports Pike and Williamson's (1961) suggestion that it be accorded suprageneric, rather than generic, status.

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LITERATURE CITED

FROST, N.
1936. Decapod larvae from Newfoundland waters. Div. Fish. Res., Newfoundland, Rep. Faunistic Ser. 1:11-24.

GURNEY, R.
1942. Larvae of decapod Crustacea. Ray Soc. (Lond.) Publ. 129, 306 p.

HAYNES, E.
1976. Description of zoeae of coonstripe shrimp, *Pandalus hypsinotus*, reared in the laboratory. Fish. Bull., U.S. 74:323-342.
1978. Description of larvae of a hippolytid shrimp, *Lebbeus groenlandicus*, reared in situ in Kachemak Bay, Alaska. Fish. Bull., U.S. 76:457-465.
1980. Stage I zoeae of a crangonid shrimp, *Crangon franciscorum angustimana*, hatched from ovigerous females collected in Kachemak Bay, Alaska. Fish. Bull., U.S. 77:991-995.

HOLTHUIS, L. B.
1947. The Decapoda of the Siboga Expedition. Part IX. The Hippolytidae and Rhynchocinetidae collected by the Siboga and Snellius Expeditions with remarks on other species. Siboga Exped. 140, Monogr. 39a[8], 100 p.

IVANOV, B. G.
1971. The larvae of some eastern shrimp in relation to their taxonomic status. (Lichinki nekotorykh dal'nevostochnykh krevetok v svyazi s ikh sistematicheskim polozheniem). Zool. Zh. 50:657-665. (Translated from Russ., U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Div. Foreign Fish., Transl. IPST 651162, TT 72-50044).

KRØYER, H.
1842. Monografisk Fremstilling af Slaegten Hippolyte's nordiske Arter. Med Bidrag til Decapodernes Udviklingshistorie. K. Dan. Vidensk. Selsk. Naturvidensk. Math. Afh. Kbh. 9:209-360. (This work has not been seen by the author.)

LEBOUR, M. V.
1931. The larvae of the Plymouth Caridea. II. The larvae of the Hippolytidae. Proc. Zool. Soc. Lond. 1931, p. 6-9.
1932. The larval stages of the Plymouth Caridea. III: The larval stages of *Spirontocaris cranchii* (Leach). Proc. Zool. Soc. Lond. 1932, p. 131-137.
1936. Notes on the Plymouth species of *Spirontocaris* (Crustacea). Proc. Zool. Soc. Lond. 1936, p. 89-104.
1937. The newly hatched larva of *Spirontocaris spinus* (Sowerby) var. *Lilljeborgi* Danielssen. J. Mar. Biol. Assoc. U.K. 22:101-104.
1940. The larvae of the British species of *Spirontocaris* and their relation to *Thor* (Crustacea Decapoda). J. Mar. Biol. Assoc. U.K. 24:505-514.

MAKAROV, R. R.
1967. Larvae of the shrimps and crabs of the West Kamchatkan Shelf and their distribution (Lichinki krevetok, rakov-otshel'nikov i krabov zapadnokamchatskogo shel'fa i ikh raspredelenie). (Natl. Lending Libr. Sci. Technol., Boston Spa, Yorkshire, Engl., 199 p.)

NEEDLER, A. B.
1934. Larvae of some British Columbia Hippolytidae. Contrib. Can. Biol. Fish., New Ser. 8:237-242.

PIKE, R. B., AND D. I. WILLIAMSON.
1961. The larvae of *Spirontocaris* and related genera (Decapoda, Hippolytidae). Crustaceana 2:187-208.

STEPHENSEN, K.
1916. Zoogeographical investigations of certain fjords in southern Greenland with special reference to Crustacea, Pycnogonida and Echinodermata including a list of Alcyonaria and Pisces. Medd. Grønl. 53:230-378.
1935. Crustacea, Decapoda. The Godthaab Expedition, 1928. Medd. Grønl. 80:1-94.

WEBB, G. E.
1921. The larvae of the Decapoda Macrura and Anomura of Plymouth. J. Mar. Biol. Assoc. U.K., New Ser. 12: 385-417.

WILLIAMSON, D. I.
1957. Crustacea, Decapoda: Larvae. V. Caridea, Family Hippolytidae. Fiches Identification Zooplancton 68, 5 p.

FEEDING BEHAVIOR AND BIOLOGY OF YOUNG SANDBAR SHARKS, *CARCHARHINUS PLUMBEUS* (PISCES, CARCHARHINIDAE), IN CHINCOTEAGUE BAY, VIRGINIA[1]

ROBERT J. MEDVED[2] AND JOSEPH A. MARSHALL[3]

ABSTRACT

During the summers of 1977, 1978, and 1979 the feeding behavior and biology of young sandbar sharks were investigated in Chincoteague Bay, Virginia, using catch data obtained from rod and reel fishing. Mean catch per unit effort for the study was 1.02 sharks per hour, but yearly differences in catch per unit effort were found. Sandbar sharks were not caught before the first week in June despite substantial fishing effort prior to this time, both in 1977 and 1978. Catch per unit effort was higher at night than during the day but was not related to tidal current stage or speed. Captures were made at surface, mid, and bottom fishing depths. During the day, catch per unit effort was highest at the bottom fishing depth but did not differ among the three depths during the night. The blue crab, *Callinectes sapidus*, was found in 41.3% of the stomachs examined; 20% of the stomachs were empty, and the remainder contained various crustaceans and fishes. The proportion of empty or nearly empty stomachs was greater for night captures than for day captures. Yearly differences in sex ratio existed and the total length distribution of sharks measured suggested the presence of relatively distinct size classes.

The natural history of the sandbar shark, *Carcharhinus plumbeus*, has received considerable attention and is relatively well known. Tag returns (Casey 1976) and analysis of commercial shark fishery records (Springer 1960) have provided valuable information on the distribution and long-term movements of this species. These studies show the sandbar shark to be an abundant, migratory shark distributed in the western North Atlantic from Cape Cod, Mass., to West Palm Beach, Fla., during the summer and from the Carolinas into the Gulf of Mexico in the winter. From spring until late fall, young sandbar sharks spend much of their time along the mid-Atlantic coast in nursery areas consisting of shallow bays and sounds. In late fall the young move farther offshore and south to wintering grounds between North Carolina and Florida. According to Casey (1976), the young may repeat this cycle for up to 5 yr and then begin to occupy areas farther offshore and undertake longer north-south migrations. Other studies have made contributions concerning growth (Wass 1973), reproduction (Taniuchi 1971), and general ecology (Bigelow and Schroeder 1948; Clark and von Schmidt 1965; Bass et al. 1973; Lawler 1977).

One area in which information is lacking, not only for this species but for sharks in general, concerns feeding behavior. Although work has been conducted on the prey items of sharks (Bigelow and Schroeder 1948) and the role of various sensory modalities in locating prey (Hobson 1963; Kleerekoper 1969; Myrberg et al. 1976; Hodgson and Mathewson 1978; Kalmijn 1978), these areas have received little attention and are little understood. Other areas of feeding behavior such as food requirements and feeding activity have received even less attention.

The specific objective of this study was to determine patterns of feeding activity of young sandbar sharks in relation to the time of day, tidal cycle, and vertical positions within the water column. Because information on sandbar sharks in nursery areas is scarce, data concerning the food items, abundance, sex ratio, and age-class composition of this species in Chincoteague Bay are also presented.

METHODS

This study was conducted from early May through late August during 1977 and 1978 and on

[1]Contribution No. 1, Wallops Island Marine Science Center.

[2]Department of Biology, West Virginia University, Morgantown, W. Va.; present address: Graduate School of Oceanography, University of Rhode Island, Kingston, RI 02881.

[3]Department of Biology, West Virginia University, Morgantown, WV 26506.

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12 July 1979 in the lower portion of Chincoteague Bay, Va. (Figure 1). Located within the summer distribution of this species, the bay supports a relatively large number of young sandbar sharks from early June through September (pers. obs.). Average water depth of the bay is 2 m, but many areas with strong current flow have depths as great as 12 m. A tidal inlet connects the bay with the Atlantic Ocean and tidal range varies from 0.75 to 2.00 m. Salt marshes with numerous tidal creeks, brackish to seawater salinities, and other conditions which seem typical of the nursery grounds of this shark along the middle Atlantic coast also characterize the area.

A 4.9 m outboard motorboat was used as a fishing platform and sharks were caught using sport fishing rods with 3/0 Penn[4] reels. Terminal tackle consisted of a 0.3 m wire leader with a straight-shank, ball-eye fishing hook. To increase fishing effort, two leaders were attached (0.5 m apart) on each fishing line. To facilitate captures over the entire size range of sharks in the area, each line was rigged with a 3/0 and a 8/0 hook. A lead sinker or cork float was attached to adjust the lines to the desired fishing depth. Cut pieces of freshly frozen Atlantic menhaden, *Brevoortia tyrannus*, were used as bait and each hook was rebaited hourly. Nothing was thrown into the water to attract sharks except the bait. Upon capture each shark was brought into the boat where it was identified, sexed, and measured. The shark was then either tagged and released or sacrificed for stomach content analysis.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

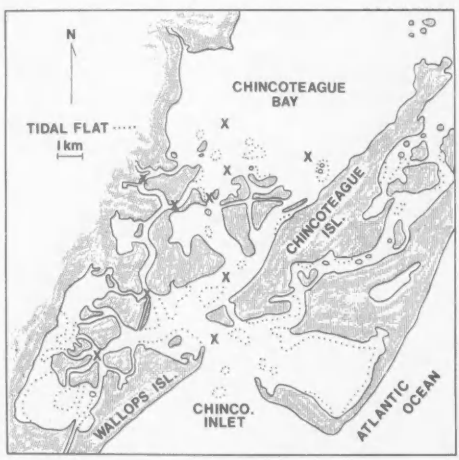

FIGURE 1.—Chart of the Chincoteague Bay study area (modified from National Ocean Survey Charts 12210 and 12211). x's give the locations of the 10 24-h fishing stations.

The type of fishing conducted fell into two categories. On 10 occasions, continuous fishing stations of approximately 24-h duration were completed (three in 1977, six in 1978, and one in 1979). These stations occurred at 10 different locations (Figure 1), each with a water depth >3 m. On all stations, the boat was anchored and three rods (rigged and baited as described above) were used with a rod fishing at the surface, middepth, and bottom. Fishing technique was standardized from station to station. After catching a shark, the rod was immediately replaced by another so that fishing effort was not interrupted. On 52 other occasions (20 in 1977 and 32 in 1978), shorter fishing periods were completed at randomly selected locations. The duration of these fishing periods and the time of day that they were conducted varied, but in a random fashion. The same fishing gear was employed at these times, but shallow as well as deep areas were fished. These shorter fishing periods are hereafter referred to as miscellaneous fishing stations. During both types of fishing, data concerning tidal current flow and water temperature were collected.

Strikes by fishes not captured were not included in the analysis of data. For each fishing station, catch per unit of effort (CPUE) was calculated by dividing the total number of sharks caught by the total number of hours spent fishing. CPUE is expressed as the number of sandbar sharks caught per hour of fishing using the three fishing rods previously described. CPUE was also calculated for various comparison categories within fishing stations such as day and night periods. For comparison categories involving fishing depth, CPUE at each depth was based on one fishing rod. Where mean CPUE is referred to in the results, the value is the arithmetic mean of CPUE values calculated for each fishing station. Because values of CPUE were not normally distributed, nonparametric methods of data analysis were employed. The tests used are described by Hollander and Wolfe (1973). Due to the large number of statistical comparisons made, many of the test names and probability values are given in tables rather than in the text of the results.

RESULTS

A total of 73 h from 17 fishing stations conducted in May 1977 and 1978 resulted in no catches. The first catch occurred on 6 June 1977 and on 1 June 1978 at water temperatures of 20.5° C and 21.0° C, respectively. After the initial catch, sandbar sharks were caught consistently and CPUE did not differ significantly among June, July, and August during either year (Table 1).

The number of catches and hours of fishing conducted after the arrival of sandbar sharks are summarized in Table 2. A total of 318 sharks were caught in 478 h of fishing. Mean CPUE for the 62 fishing stations was 1.02 sandbar sharks/h. CPUE varied among the 3 study yr (Table 3). CPUE in 1979 was 2.06 sandbar sharks/h, but was based on only one 24-h fishing station. In 1977 and 1978, CPUE was based on numerous fishing stations and was significantly higher in 1977.

Sandbar sharks were caught during all hours of the day and night. CPUE was calculated at 1-h intervals for each 24-h fishing station, but because of the relatively small sample size, numerous observations of zero CPUE, and great station-to-station variation in CPUE, these data were not sufficient for a statistical analysis of diel rhythmicity. Visual inspection did suggest a day-night difference in CPUE. On all but one 24-h station, CPUE was higher during the night than during the day. Grouping the data on this more general level and treating day and night observations (on CPUE) as samples paired on fishing station indicates CPUE was significantly higher during the night than during the day (Table 4).

CPUE did not differ significantly between flood and ebb tidal current periods (Table 4). During both current periods CPUE was higher during the night than during the day, but, because of multiple testing on the same data, the probability values given for the tests should be considered as only rough approximations (Table 4).

Catch data were grouped into four tidal current speed categories. Sandbar sharks were caught over the entire range of current speeds recorded during 24-h stations and CPUE was not significantly different among the four current speed categories (Table 5).

CPUE was calculated for the three fishing depths used during 24-h fishing stations. Although sandbar sharks were caught at all three depths, CPUE differed significantly among them (Friedman test, $P = 0.02$) and was higher at the bottom than at the surface or middepth. CPUE did not differ significantly between the surface and middepth (Table 6). The difference in CPUE among the depths was not the same for both day

TABLE 1.—Summary of fishing data for the 3 study mo of 1977 and 1978. The value given for "Mean rank" is the mean of the ranks assigned to the observations on CPUE in a Kruskal-Wallis test for differences in CPUE among months within the indicated year.

Year	Month	No. of fishing stations	Mean CPUE (sharks/h)	Mean rank	*P*-value
1977	June	13	1.46	16.1	
	July	5	1.63	13.4	0.46
	Aug.	5	.92	13.4	
1978	June	17	.63	17.3	
	July	12	.64	20.2	.47
	Aug.	9	1.21	22.8	

TABLE 2.—Summary of fishing data for 24-h stations, miscellaneous stations, and all stations combined.

Stations	Hours of fishing	No. of sharks caught	No. of stations	Mean CPUE (sharks/h)
24 h	232	160	10	0.67
Miscellaneous	246	158	52	1.07
Overall	478	318	62	1.02

TABLE 3.—Summary of fishing data for each study year. The value given for "Mean rank" is the mean of the ranks assigned to the observations on CPUE in a Mann-Whitney *U*-test.

Year	Hours of fishing	No. of sharks caught	No. of fishing stations	Mean CPUE (sharks/h)	Mean rank	*P*-value (2-tail test)
1977	128	119	23	1.39	39.2	0.005
1978	325	148	38	.76	26.0	
1979	25	51	1	2.06		

TABLE 4.—Summary of fishing data for various periods during 10 24-h fishing stations. The values given for "Rank sums" are the sums of the positive and negative differences of paired observations on CPUE in a Wilcoxon signed rank test. Differences for day-night and for day-night by current stage categories were for CPUE during the night minus CPUE during the day. Differences for the flood-ebb category were for CPUE during flood minus CPUE during ebb. Dusk and dawn periods were split equally between day and night categories.

Period	Hours of fishing	No. of sharks caught	Mean CPUE (shark/h)	Rank sums (+)	Rank sums (−)	*P*-value (2-tail test)
Day	143	85	0.56	48	7	0.04
Night	89	75	.66			
Flood	115	90	.75	39	16	.23
Ebb	117	70	.55			
Flood-day	76	49	.62	45	10	[1].08
Flood-night	38	41	.78			
Ebb-day	67	36	.41	47	8	[1].04
Ebb-night	51	34	.65			

[1]Probabilities should be considered as rough approximations because of multiple testing on the same data.

TABLE 5.—Summary of fishing data for tidal current speed categories during the eight 24-h fishing stations in which current speed was recorded. The value given for "Rank sum" is the sum of the ranks assigned to the observations on CPUE for that current speed category in a Friedman test.

Current speed (m/min)	Hours of fishing	No. of sharks caught	Mean CPUE (shark/h)	Rank sum	*P*-value
<10	36.5	25	0.65	24.0	
10-20	42.5	20	.51	16.5	
20-30	52.0	35	.64	17.5	$0.30<P<0.50$
>30	55.5	42	.63	22.0	

TABLE 6.—Summary of fishing data for the three fishing depths used during the 10 24-h fishing stations. The value for "Rank sum" is the sum of the ranks assigned to the observations on CPUE for that fishing depth in a Friedman test. Vertical lines are used to indicate significantly different CPUE ($\alpha = 0.05$, multiple comparisons based on Friedman rank sums).

Fishing depth	Hours of fishing	No. of sharks caught	Mean CPUE (shark/h)	Rank sum
Surface	232	32	0.11	15.5
Middepth	232	42	.16	17.0
Bottom	232	85	.37	27.5

and night fishing periods. During the day, CPUE differed significantly among fishing depths and was highest at the bottom. In contrast, during the night no difference in CPUE was found among fishing depths (Table 7). At surface and middepth CPUE was substantially higher during the night than during the day on 9 out of 10 and 8 out of 10 fishing stations, respectively. In contrast, at the bottom CPUE differed little between day and night periods and was not consistently higher or lower during the night. These observations suggest that the above difference between day and night periods (i.e., depth differences in CPUE during the day but not during the night) was a result of increased CPUE at surface and middepth during the night rather than a decrease in CPUE at the bottom.

TABLE 7.—Summary of fishing data for time period-fishing depth categories during the 10 24-h fishing stations. The value given for "Rank sum" is the sum of the ranks assigned to the observations on CPUE for that category in a Friedman test. Vertical lines are used to indicate significantly different CPUE ($\alpha = 0.05$, multiple comparisons based on Friedman rank sums).

Time period-fishing depth	Hours of fishing	No. of sharks caught	Mean CPUE (shark/h)	Rank sum
Day-surface	143	12	0.07	16.5
Day-middepth	143	21	.13	26.5
Day-bottom	143	52	.37	51.0
Night-surface	89	20	.22	32.5
Night-middepth	89	21	.23	38.5
Night-bottom	89	33	.36	48.5

The stomach contents of 80 sandbar sharks were examined to identify food items (Table 8). Items that could be identified included small crustaceans and fishes that are abundant in the study area (pers. obs.). The blue crab, *Callinectes sapidus*, of all sizes was found in 41% of the stomachs examined (and in over 52% of the stomachs not empty). Two or more different food items were found in 14 stomachs and several stomachs contained unidentifiable items but were very nearly empty. The proportion of empty or nearly empty stomachs (15 empty out of 27 examined) for sandbar sharks caught during the night was significantly greater than the proportion (16 empty out of 53 examined) for sharks caught during the day (2-tailed chi-square test for differences in probabilities, $P = 0.04$). Stomach contents were, in general, similar for the 3 study yr, both sexes, all sizes of sharks, and tidal current and capture depth categories.

The total number of male and female sharks caught (over all 3 yr) did not differ significantly, but yearly differences in sex ratio were found (Table 9). During 1978 and 1979 about equal numbers of male and female sandbar sharks were caught, but in 1977 significantly more females than males were caught. Sex ratios were consistent among the 3 study mo (June, July, and

TABLE 8.—Stomach contents of 80 young sandbar sharks.

Stomach contents	No. of stomachs found in	Percent of stomachs found in
Blue crab, *Callinectes sapidus*	33	41.3
Unidentified fish	9	11.3
Mantis shrimp, *Squilla* sp.	8	10.0
American eel, *Anguilla rostrata*	7	8.8
Calico crab, *Ovalipes ocellatus*	6	7.5
Puffer, *Tetraodon maculatus*	4	5.0
Atlantic menhaden, *Brevoortia tyrannus*	3	3.8
Rock crab, *Cancer irroratus*	3	3.8
Unidentifiable material	3	3.8
Unidentified crustacean	1	1.3
Unidentified crab	1	1.3
Unidentified shrimp	1	1.3
Bluefish, *Pomatomus saltatrix*	1	1.3
Spot, *Leiostomus xanthurus*	1	1.3
Mummichog, *Fundulus heteroclitus*	1	1.3
Empty stomachs	16	20.0

TABLE 9.—Number of male and female sandbar sharks caught and probabilities for chi-square goodness of fit test (2-tailed) for each year and the entire study.

Year	No. of males	No. of females	*P*-value
1977	24	48	<0.01
1978	60	58	$0.80<P<0.90$
1979	28	22	$.30<P<0.50$
Total	112	128	$.30<P<0.50$

August) both in 1977 and 1978, i.e., unbalanced in 1977 but balanced in 1978. For all study years taken together, the number of male sandbar sharks caught did not differ significantly from the number of females caught during day or night periods, during flood or ebb current periods, at any of the three fishing depths, or for any of the four current speed categories (2-tailed chi-square goodness of fit Test, $\alpha = 0.05$).

With the exception of one sandbar shark (137.0 cm TL), the catch ranged from 60.0 to 112.5 cm TL. The length distributions for 1977 and 1978 are presented in Figure 2. Both distributions were based on relatively small numbers of sandbar sharks and are no doubt rough approximations of the actual size distributions. The fact that the distributions were not continuous and were characterized by several well-defined peaks does, however, suggest that in both years, the population of sandbar sharks consisted of relatively distinct size classes. Based on only visual inspection of the distributions, it appears that at least 3 and possibly as many as 5 different size classes may have been present. In general, similar size distributions were found for sex, light, tidal current stage and speed, and fishing depth categories.

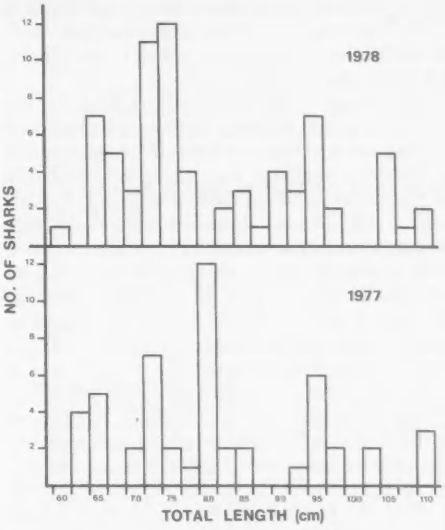

FIGURE 2.—Frequency distribution for total length of sandbar sharks caught and measured in 1977 and 1978. The total length given for each interval is the beginning length for that 2.5 cm wide interval.

DISCUSSION

Despite many hours of fishing, no sandbar sharks were caught before the first week of June either in 1977 or 1978, suggesting they were not present in the area during this time. Local fishermen who commonly catch numerous sharks in their gill nets also did not encounter sandbar sharks over this period; it appears that few, if any, sandbar sharks had migrated into the Chincoteague Bay area before the first week in June during these years. The consistency in CPUE among months within each year (Table 1) suggests that the abundance of sandbar sharks remained relatively constant in June, July, and August.

The mean CPUE of 1.02 sandbar sharks/h for the study indicates that the Chincoteague Bay area supports a large number of young sandbar sharks during the summer. The factors responsible for yearly differences in CPUE (Table 3) are unknown. Because fishing locations and times were selected in a random fashion and fishing technique was standardized over the entire study, it is unlikely that the differences were a result of the methods employed. Year-to-year changes in population numbers and/or shifts in distribution resulting in local differences in abundance may have been involved.

The significantly higher CPUE experienced during the night (Table 4) may relate to day-night differences in 1) the abundance of sandbar sharks in Chincoteague Bay, 2) the availability of prey, 3) the visual "attractiveness" of the bait, or 4) the feeding activity of young sandbar sharks.

Movements of sandbar sharks out of Chincoteague Bay to adjacent ocean waters during the day and back into the bay during the night could result in the observed differences. The movements of 23 sandbar sharks tracked in this area (Medved unpubl. data) were strongly oriented in the direction of tidal current flow and do not suggest a day-night pattern of movement into and out of the bay.

A decrease in the availability of various prey species could also account for increased CPUE during the night. Observations confirmed by local crab fishermen indicate that the blue crab (the most common food item found in the stomachs examined) is frequently found swimming near the water's surface during the night but rarely during

the day. This difference in behavior would seem to make the blue crab more accessible and would probably tend to decrease rather than increase CPUE during the night.

Differences in the visual attractiveness of the bait used to catch sharks may have existed, but the limited visibility (<1 m) in the turbid waters of the area suggests that vision was probably of little importance in feeding behavior. Experiments conducted on various species (Hobson 1963; Hodgson and Mathewson 1978; Kalmijn 1978) have shown the ability of sharks to locate food by means other than vision and that feeding behavior is directed towards almost any object present in a high concentration of olfactory material. These experiments indicate that the importance of vision may be only to direct the final act of feeding. It appears doubtful that day-night differences in the visual attractiveness of the bait were responsible for increased CPUE during the night.

Finally, the night hours may simply be a period of increased feeding activity for young sandbar sharks in this area. The existence of such a diel pattern would not be surprising in that similar rhythmicity for various activities (including feeding) has been reported for several sharks (Springer 1963, see footnote 5; Randall 1967; Hobson 1968; Nelson and Johnson 1970; Myrberg and Gruber 1974; Finstad and Nelson 1975; Sciarrotta and Nelson 1977).

Numerous catches at surface and middepth (Table 6) suggest that the young of this species occur throughout the vertical range of the water column. This would appear to be in conflict with Springer's (1960) statement that sandbar sharks are properly considered "ground sharks," rarely seen at or near the surface. However, most of Springer's observations were apparently made on adult sandbar sharks. The conflict may simply indicate differences between the young and adults of this species. The increase in CPUE at surface and middepth at night (Table 7) suggests that the tendency of sandbar sharks to move into these areas may have been greater at night and possibly related to the movements of blue crabs discussed earlier.

In general, food items taken by this shark (Table 8) agree with those reported by other authors (Bigelow and Schroeder 1948; Springer 1960; Clark and von Schmidt 1965; Bass et al. 1973; Lawler 1977). The fact that the blue crab was by far the major prey item may simply reflect its abundance in the area rather than a specific food preference. Wass (1973) indicated that food is retained within the stomachs of sandbar sharks for periods of 2-4 d or more, depending on the consistency of the item. The relatively large proportion of empty stomachs observed in this study would then indicate that the young of this species may frequently go at least several days without feeding. Whether this is by choice or imposed by difficulties in capturing food is uncertain. The higher proportion of empty stomachs observed for sandbar sharks caught during the night than for those caught during the day may relate to the possible day-night difference in feeding activity previously mentioned.

Selectivity in the fishing method employed may account for the observed yearly differences in sex ratio (Table 9). Assuming equal numbers of both sexes in the area, the method must have been selective for females in 1977 but not in 1978 and 1979. Considering that the same methods were employed in all years, it appears that the proportion of male and female sharks utilizing the area may have varied among years.

It seems that sandbar sharks >112.5 cm TL rarely occurred in the study area (Figure 2). The failure to capture larger sharks was not felt to be related to the fishing method because this method has yielded numerous large sandbar sharks in offshore areas (pers. obs.). A period of approximately 9 mo separates successive year classes of sandbar sharks (Springer 1960), and age determinations using vertebral annuli indicate relatively rapid rates of growth for the first several year classes (Lawler 1977). Lawler's growth rates suggest that the relatively distinct size classes apparent in this study were probably a reflection of the various year classes of sandbar sharks present in the area. The impression of the existence of 3 to 5 different age-classes given by the size distributions also agrees with Casey's (1976) contention that young sandbar sharks may occupy nursery ground areas for up to 5 yr before moving farther offshore.

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[5]Springer, S. 1943. Sharks and their behavior. Special report to the Coordinator of Research and Development, U.S.N. Emergency Rescue Equipment Section.

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LITERATURE CITED

BASS, A. J., J. D. D'AUBREY, AND N. KASTNASAMY.
1973. Sharks of the east coast of southern Africa. I. The genus *Carcharhinus* (Carcharhinidae). S. Afr. Assoc. Mar. Biol. Res. Invest. Rep. 33, 168 p.

BIGELOW, H. B., AND W. C. SCHROEDER.
1948. Sharks. *In* A. E. Parr and Y. H. Olsen (editors), Fishes of the western North Atlantic, Part one, p. 59-576. Mem. Sears Found. Mar. Res. Yale Univ. 1.

CASEY, J. G.
1976. Migration and abundance of sharks along the Atlantic Coast. *In* W. Seaman, Jr. (editor), Sharks and man—a perspective, p. 13-14. Fla. Sea Grant Program, Rep. 10.

CLARK, E., AND K. VON SCHMIDT.
1965. Sharks of the central gulf coast of Florida. Bull. Mar. Sci. 15:13-83.

FINSTAD, W. O., AND D. R. NELSON.
1975. Circadian activity rhythm in the horn shark, *Heterodontus francisci*: effect of light intensity. Bull. South. Calif. Acad. Sci. 74:20-26.

HOBSON, E. S.
1963. Feeding behavior in three species of sharks. Pac. Sci. 17:171-194.
1968. Predatory behavior of some shore fishes in the Gulf of California. U.S. Fish Wildl. Serv., Res. Rep. 73, 92 p.

HODGSON, E. S., AND R. F. MATHEWSON.
1978. Electrophysiological studies of chemoreception in elasmobranchs. *In* R. Mathewson and E. S. Hodgson (editors), Sensory biology of sharks, skates, and rays, p.227-267. U.S. Gov. Print. Off.

HOLLANDER, M., AND D. A. WOLFE.
1973. Nonparametric statistical methods. Wiley, N.Y., 503 p.

KALMIJN, A. J.
1978. Electric and magnetic sensory world of sharks, skates, and rays. *In* R. Mathewson and E. Hodgson (editors), Sensory biology of sharks, skates, and rays, p. 507-528. U.S. Gov. Print. Off.

KLEEREKOPER, H.
1969. Olfaction in fishes. Indiana Univ. Press, Bloomington, 222 p.

LAWLER, E.
1977. The biology of the sandbar sharks *Carcharhinus plumbeus* (Nardo, 1827) in the lower Chesapeake Bay and adjacent waters. Masters Thesis, Va. Inst. Mar. Sci., Gloucester Point.

MYRBERG, A. A., JR., AND S. H. GRUBER.
1974. The behavior of the bonnethead shark, *Sphyrna tiburo*. Copeia 1974:358-274.

MYRBERG, A. A., JR., C. R. GORDON, AND A. P. KLIMLEY.
1976. Attraction of free ranging sharks by low frequency sound, with comments on its biological significance. *In* A. Schuijf and A. D. Hawkins (editors), Sound reception in fish, p. 205-228. Elsevier, Amst.

NELSON, D. R., AND R. H. JOHNSON.
1970. Diel activity rhythms in the nocturnal, bottom-dwelling sharks, *Heterodontus francisci* and *Cephaloscyllium ventriosum*. Copeia 1970:732-739.

RANDALL, J. E.
1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. (Miami) 5:665-847.

SCIARROTTA, T. C., AND D. R. NELSON.
1977. Diel behavior of the blue shark, *Prionace glauca*, near Santa Catalina Island, California. Fish. Bull., U.S. 75:519-528.

SPRINGER, S.
1960. Natural history of the sandbar shark, *Eulamia milberti*. U.S. Fish Wildl. Serv., Fish. Bull. 61:1-38.
1963. Field observations on large sharks of the Florida-Caribbean region. *In* P. W. Gilbert (editor), Sharks and survival, p. 95-114. D. C. Heath and Co., Boston.

TANIUCHI, T.
1971. Reproduction of the sandbar shark (*Carcharhinus milberti*) in the East China Sea. Jpn. J. Ichthyol. 18:94-98.

WASS, R. C.
1973. Size, growth, and reproduction of the sandbar shark, *Carcharhinus milberti*, in Hawaii. Pac. Sci. 27:305-318.

SEASONAL CHANGES IN SOFT-BODY COMPONENT INDICES AND ENERGY RESERVES IN THE ATLANTIC DEEP-SEA SCALLOP, *PLACOPECTEN MAGELLANICUS*[1]

WILLIAM E. ROBINSON,[2] WILLIAM E. WEHLING,[3] M. PATRICIA MORSE,[3] AND GUY C. MCLEOD[4]

ABSTRACT

The relationship between the energy storage cycle and gametogenesis was investigated over a 1-year period (March 1979-March 1980) in a population of the Atlantic deep-sea scallop, *Placopecten magellanicus*, from Boothbay, Maine. Soft body component indices, dry weights, lipid, and carbohydrate levels were measured in digestive gland, adductor muscle components, and gonadal tissue. In addition, mantle, mantle edge, foot, and kidney tissues were examined histochemically for glycogen and lipid content. Gametogenesis began in early winter (December-January) during a period when energy reserves and tissue indices were falling. Gonadal growth occurred concurrently with increases in body component indices, dry weights, and replenishment of lipid and carbohydrate levels in the digestive gland and adductor muscle (January-March). The accumulated springtime energy reserves in somatic tissues were lost in the late spring-summer, as maturation of gametes was completed. Following spawning in mid-September, a slight recovery of energy reserve levels and body component index values was evident for the digestive gland and quick component of the adductor muscle. Recovery did not occur in the gonad. Energy reserves, body component indices, and dry weights all declined throughout the late fall and early winter months. A buildup of energy reserves in the early spring appears essential for the later completion of gonadal maturation. Similarly, the autumn recovery of energy reserves within the somatic tissue may be important for the subsequent initiation of gametogenesis in early winter, as well as for meeting metabolic demands during the period of low food-availability.

The Atlantic deep-sea scallop, *Placopecten magellanicus* (Gmelin), supports an extensive commercial fishery throughout most of its western Atlantic range from the Strait of Belle Isle, Newfoundland, to Cape Hatteras, N.C. (Posgay 1957; Altobello et al. 1977; Serchuk et al. 1979). In spite of its economic importance, the underlying factors which affect reproductive success are poorly understood although the basic reproductive biology is well documented. The annual cycle of gametogenesis has been described both macroscopically (Coe 1945) and microscopically (Naidu 1970). Spawning seasons have been identified throughout most of the scallop's geographical range (Dickie 1955; Posgay and Norman 1958; Naidu 1970; Merrill and Edwards 1976). Larval development has been followed in the laboratory through settlement (Baird 1953; Culliney 1974; Drew 1906) and temperature and salinity effects on development have been investigated (Culliney 1974). The lack of consistent year-class recruitment, however, probably reflects the importance of environmental influences on reproductive success (Dickie 1955; Serchuk et al. 1979).

As an initial step toward a better understanding of reproductive success in any invertebrate species, the relationship between the buildup and utilization of energy reserves and the annual cycle of gametogenesis and spawning should be investigated (Giese and Pearse 1974). Thompson (1977) undertook such an approach using Atlantic deep-sea scallops collected from three populations in southeast Newfoundland. Although his main emphasis was on the seasonal changes in blood chemistry, biochemical analyses for glycogen, lipid, and protein levels were conducted on both gonadal and somatic tissues. Other contributions to an understanding of the energy reserve-reproductive cycle relationship have been made. Naidu (1970) presented gonad wet weight data, broken

[1]Contribution No. 97, Marine Science Institute, Northeastern University.

[2]Marine Science Institute, Northeastern University, Nahant, Mass., and Department of Biology, Northeastern University, Boston, Mass.; present address: New England Aquarium, Research Department, Central Wharf, Boston, MA 02110.

[3]Marine Science Institute, Northeastern University, Nahant, MA 01908 and Department of Biology, Northeastern University, Boston, MA 02115.

[4]New England Aquarium, Central Wharf, Boston, MA 02110.

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down by scallop age, over a 2-yr period, in addition to a histological description of the gametogenic cycle. Seasonal changes in total fat, sterol, and unsaponifiable fat within the adductor muscle have been described by Idler et al. (1964), and six major phospholipids identified from whole-body extracts by Shieh (1968).

The present study was undertaken to identify and localize the major energy reserves of *P. magellanicus*, to follow the levels of these reserves within each identified storage tissue over a 1-yr period, and to monitor the gametogenic cycle histologically.

MATERIALS AND METHODS

Deep-sea scallops were collected by divers at approximately 6-8 wk intervals from natural beds at the mouth of the Damariscotta River, off Farnham Pt., Linekin Neck, Boothbay, Maine, in 10-30 m of water. Deep-sea scallops ranged from 79.8 to 163.0 mm shell height ($\bar{X}$ = 119.0, SD = 17.5 mm, N = 165), although individual size varied considerably within each sample. Animals were transported to the laboratory in chilled seawater and maintained overnight in a running seawater system. Twenty deep-sea scallops (10 of each sex whenever possible) were chosen for subsequent analyses. Shell height was measured for each deep-sea scallop prior to dissection. Wet weights were recorded for total body (exclusive of mantle cavity water), shell, both catch and quick components of the adductor muscle, digestive gland, and "gonadal mass" (defined as all gonadal tissue, overlying epidermis, inclusive connective tissue, and intestinal loop). The contents of the intestinal loop were gently squeezed out prior to weighing. Similarly, the stomach and surrounding digestive gland were split open, and all food material flushed out with seawater. Gastric shield and crystalline style were excluded from digestive gland and gonadal mass wet weights. Tissues were individually frozen and stored at −20° C for subsequent biochemical analyses.

Body Component Indices

Individual soft-body component indices were calculated for catch adductor (CAI), quick adductor (QAI), digestive gland (DGI), and gonadal mass (GMI) according to Giese et al. (1967): body component index = wet weight of body component ÷ total wet body weight. Total wet body weight was determined by subtracting wet shell weight from total wet weight, and therefore includes the weight of extrapallial fluid which would have been lost if body weights were determined following separation of the animal from its valves. Linear regression analysis of body component index values (GMI, DGI, QAI, and CAI) on shell height revealed that all indices were independent of body size within the sampled range. The use of index values for comparisons between samples containing different size distributions of deep-sea scallops was therefore justified.

Histological and Histochemical Monitoring

Following wet weight determinations, a small piece of GMI tissue was fixed in Bouin's fluid for histological examination of gametogenesis. Tissues were later dehydrated, embedded in polyester wax (Steedman 1960), sectioned at 7 μm, and stained in 2% aqueous celestin blue. Gametogenic state was characterized as either early, mid, or late developing, ripe, partially spawned, or spent, based on a shortened version of the nine stages described by Naidu (1970). During early development, gonadal follicles are predominantly empty except for a few layers of spermatocytes or a single layer of oocytes closely oppressed to the follicular wall. In middeveloping follicles, the lumen is more restricted. Oocytes are enlarged in females, whereas in males, spermatids and spermatozoa become increasingly common although spermatocytes are still predominant. The follicular lumen is occluded by mature or maturing spermatozoa and oocytes in late-developing gonads, although immature stages are common toward the periphery of the follicles. In ripe gonads, follicles are tightly packed with mature gametes. Follicles show a progressive loss of ripe gametes as spawning proceeds, ultimately becoming empty when deep-sea scallops are completely spent.

Gametogenic values were assigned to each stage (early developing = 1, middeveloping = 2, late developing = 3, ripe = 4, partially spawned = 2, spent = 0). The mode, median, and range of gametogenic values were used for comparisons between sample dates.

To insure that tissues examined biochemically were sites of major energy reserves, a variety of tissues were fixed and histochemically examined from one or two animals of each sex during each sample period. In addition to the catch and quick

components of the adductor muscle, digestive gland, and gonadal mass, analyses were made on mantle, mantle edge, foot, and kidney tissue. For glycogen staining, tissues were fixed in Rossman's fluid (Humason 1972), embedded as before, and stained with Best carmine (Humason 1972). Control slides were incubated with 1% α-amylase in 0.2 *M* phosphate buffer (pH 7.0) at 40° C for 1 h. Lipid was localized in cryostat-sectioned material, postfixed in 10% calcium-Formalin[5] fixative (Humason 1972), and stained with supersaturated Oil red *O* (Lillie and Fullmer 1976). Control slides were immersed for 10 min in 95% ethanol to remove all lipid.

Biochemical Analysis of Tissues

As a result of the routine histochemical examinations, only adductor muscle, digestive gland, and gonadal mass were chosen for biochemical determinations of lipid and carbohydrate concentrations. No other tissues contained appreciable reserves of either lipid or carbohydrate at any time during the year. Tissues from the 20 deep-sea scallops chosen on each sampling date were pooled by sex into groups of 3-10 animals depending on the size of tissue sample and time of year. The pooled samples were freeze-dried to determine wet:dry weight ratios for each tissue. Subsamples of the dried tissue were used for biochemical analyses. Lipid concentrations were determined gravimetrically after extraction in acetone-isooctane (Peterson et al. 1976). Glycogen levels were determined on each of the four tissues using the glucose-oxidase method as described by Williams and Lutz (1975). All glycogen was first converted to glucose by a 2-h incubation at 55° C in 1% amyloglucosidase (Sigma A-7255). Glucose concentrations were then measured spectrophotometrically following a 30-min incubation at 37° C with a mixture of glucose-oxidase and peroxidase (Sigma Kit 510-A). The results give the combined concentrations of both glucose and glycogen for each tissue, and will hereafter be considered "carbohydrate." Since initial results indicated that wet:dry weight ratios, lipid, and carbohydrate concentrations were not significantly different in the catch and quick components of the adductor muscle (March-April samples), analyses of the smaller catch component was discontinued.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Standard Scallop

In order to account for the influences of animal size on seasonal body changes, body component dry weights, and biochemical constituents were calculated for a "standard scallop" of 120 mm shell height. This height was close to the mean (119.0 mm) and mode (115.2 mm) for the combined yearly samples. Predictive regressions of wet tissue weight (separately for gonadal mass, digestive gland, and quick adductor) on shell height were calculated for each sex within each sample. The resulting regression equations were solved for the standard deep-sea scallop (120 mm shell height). These wet weight values were converted to estimated dry weights of each tissue using the wet:dry weight ratios. By multiplying the estimated dry weights of each tissue by the corresponding concentrations of lipid and carbohydrate, total amount of each energy reserve per tissue was calculated. These energy reserve levels were then converted to caloric equivalents using the conversion factors from Crisp (1971) (carbohydrate = 4.1 kcal/g; lipid = 9.45 kcal/g). Since the calculations for dry weight, lipid, and carbohydrate were based on mean values of pooled tissue samples and regressions of wet tissue weight on shell height, confidence limits could not be estimated for the resulting values. All results have been presented as total amount of each energy reserve per standard animal.

RESULTS

Gametogenic Cycle

During most of the year, deep-sea scallops could easily be sexed by visual examination, due to the characteristic bright pink ovaries and opaque white testes. Histological sections, however, were necessary to determine the sex of spent individuals in the September-January samples. Spent gonads were shrunken, flaccid, and lacked characteristic coloration, instead possessing semitransparent epidermal and connective tissues.

Gametogenesis, as followed histologically, conformed to the description of Naidu (1970). The seasonal gametogenic cycle, based on modal gametogenic values for each sample, is presented in Figure 1. Modal values increased throughout the winter, spring, and into the summer as gametes differentiated and ripened. Spawning was evident in 67% of the males (N = 9) and 64%

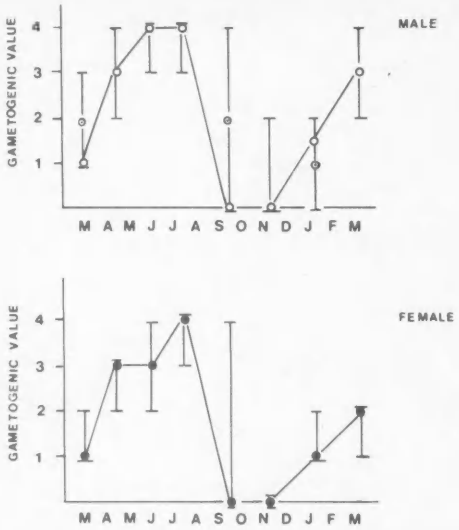

FIGURE 1.—Annual cycle of gametogenesis in *Placopecten magellanicus* based on assessment of histological sections for each sample date, March 1979-March 1980. Modal values of each sample indicated by ● for females and ○ for males. Bars = ranges. Median values indicated by ⊙ in cases where median values differ from modal values.

of the females (N = 11) from the 14 September sample, resulting in a marked drop in modal rank. Variability within the population was greatest at this time since ripe, partially spawned, and spent individuals were all present in the population. By 5 November, virtually all deep-sea scallops sampled were spawned out. In January, modal values again rose. Gonial cells were distinguishable in the follicles and characteristic gonadal coloration became evident, although a few individuals showed signs of still being only partially spawned out.

Body Component Indices

Seasonal changes in mean body component indices are plotted in Figure 2. GMI, DGI, QAI, and CAI all varied significantly with time ($P < 0.01$; analysis of covariance: body component index by sample date with scallop height as a cofactor). Similar analyses using raw tissue wet weights also point out significant changes between sampling dates ($P < 0.01$). Since differences between the sexes were not significant for any of

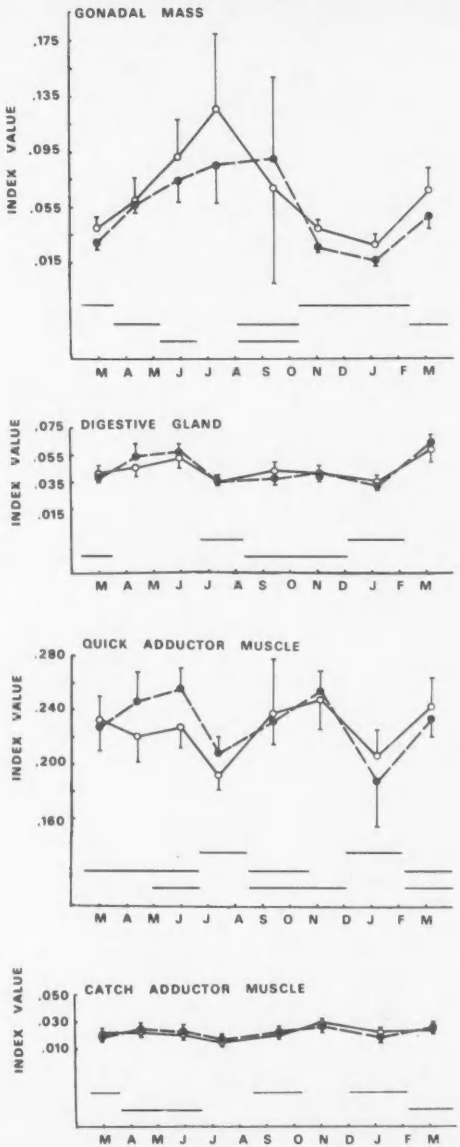

FIGURE 2.—Seasonal fluctuations in soft-body component indices for *Placopecten magellanicus*, March 1979-March 1980. Bars represent 95% confidence intervals; ■ = female; ○ = male; horizontal lines underscore samples which are not significantly different at the 95% confidence level (male and female data combined for each sample, least significant difference multiple range test).

the indices, data for each sex were combined. Multiple range tests (least significant difference) on the combined data indicated that GMI, DGI, and CAI values all rose in the spring. QAI, CAI, and DGI dropped in July, while GMI continued to rise until spawning in late summer. The September and November samples showed a recovery of QAI, CAI, and DGI, but a drop in GMI, representing a decline in the proportion of body mass attributable to the gonad following spawning. The late fall to early winter period showed a continued decline in all four indices except possibly GMI, with recovery evident by the subsequent March sample. Both GMI and modal gametogenic values (Figure 1) were much higher in the March 1980 sample than for the March sample of the previous year, probably reflecting the mild 1979-80 winter.

Differences in total wet animal weight and total wet body weight between samples were not significant (ANCOVA: $P > 0.05$). Variability of each of these components was too high to discern seasonal trends.

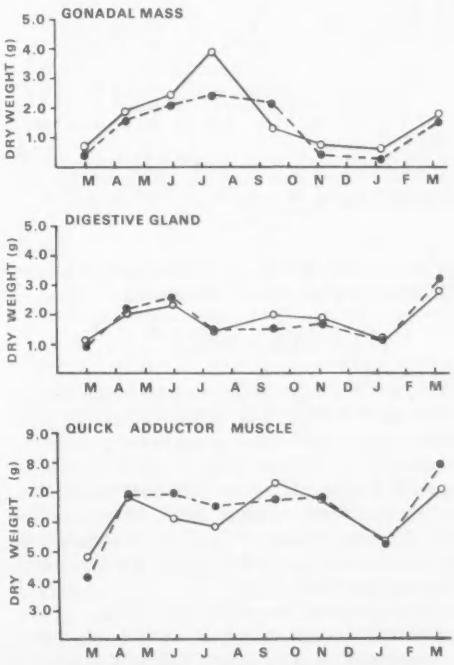

FIGURE 3.—Standard deep-sea scallop (120 mm shell height) annual tissue dry weight fluctuations. ■ = female; ○ = male.

Histochemical Localization of Energy Reserves

Appreciable concentrations of energy reserves were detected in only the adductor muscle, digestive gland, and gonadal mass. As indicated by routine histochemical examinations, a shift of energy reserves from these major areas to other tissues did not occur during the study period.

Glycogen was primarily concentrated in the adductor muscle, although significant levels were also seen in the digestive gland and the epithelium of both male and female reproductive ducts during most of the year. Concentrations were highest in the spring and early summer within the adductor muscle, ovary, and testes, but were only high in the spring within the digestive gland. Glycogen concentrations remained very low throughout the year in the mantle, mantle edge, foot, and kidney.

Lipid levels were highest throughout most of the year in the digestive gland, with peak levels in April-May 1979 and March 1980. High concentrations were also found in the ovary, increasing throughout the spring to a maximum in July, declining slightly in September, and dropping precipitously by November as a result of spawning. Significant lipid localization was not observed in any other tissue.

Dry Weight and Biochemical Analyses

Seasonal fluctuations in gonadal mass, digestive gland, and quick adductor muscle dry weights are presented in Figure 3 for standard deep-sea scallops of each sex. Following an initial increase in the weight of all tissues in the spring, gonadal dry weight continued to rise into July, whereas a concomitant decrease occurred in the weight of the adductor muscle and digestive gland. Gonadal dry weight fell throughout the autumn and early winter. The adductor and digestive gland on the other hand, recovered in the autumn to about their springtime levels, but then dropped during the early winter.

Calculated quantities of lipid and carbohydrate in tissues of standard scallops of each sex are shown in Figures 4 and 5. As with dry weights, both reserves showed an initial rise in the spring in all tissues although the rise in carbohydrate in the gonadal mass and digestive gland was slight. The amount of gonadal lipid and carbohydrate continued to increase into midsummer, whereas digestive gland lipid and adductor carbo-

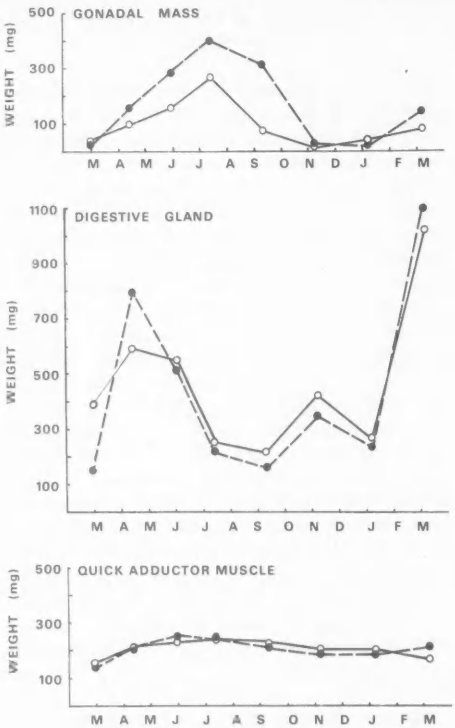

FIGURE 4.—Seasonal changes in tissue lipid content calculated for the standard deep-sea scallop (120 mm shell height). ● = female; ○ = male.

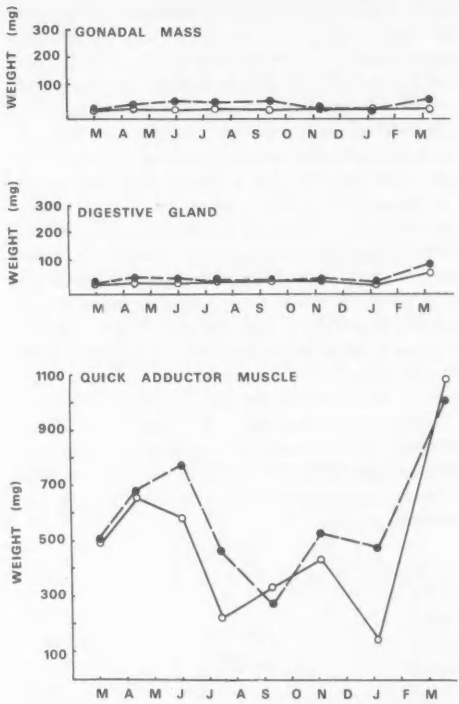

FIGURE 5.—Seasonal changes in tissue carbohydrate content calculated for the standard deep-sea scallop (120 mm shell height). ● = female; ○ = male.

hydrate fell from late spring through September. Although present at lower amounts than in the gonadal mass and digestive gland, lipid in the quick component of the adductor muscle rose in the spring-summer and dropped in the autumn-winter.

Changes in caloric equivalents (kilocalories) of energy reserves from each tissue, presented in Figure 6, reflect the changes in lipid storage in both the gonadal mass and digestive gland, and fluctuations of carbohydrate in the quick component of the adductor muscle. Differences in energy reserves between the sexes are not significant, although females tend to show higher levels and greater fluctuations in energy content throughout the year. The drop in gonadal caloric equivalents in mid-September, in addition to the drop in GMI and gonadal dry weight, is indicative of spawning within the population and is corroborated by the histological appearance of the gonads.

DISCUSSION

Of the three tissues which contain appreciable reserves of either lipid or carbohydrate, only digestive gland and adductor muscle may properly be considered "storage organs" (i.e., temporary repositories of energy-rich substances which may later be utilized to meet either metabolic or reproductive demands). Energy-rich substances within the gonad, albeit temporary, are ultimately destined for gamete production and nourishment of the developing larvae. If these substances are completely lost at spawning, as is evident for *P. magellanicus*, they should not be considered as energy reserves for the adult scallop (Giese 1966), even though resorption of gametes by some

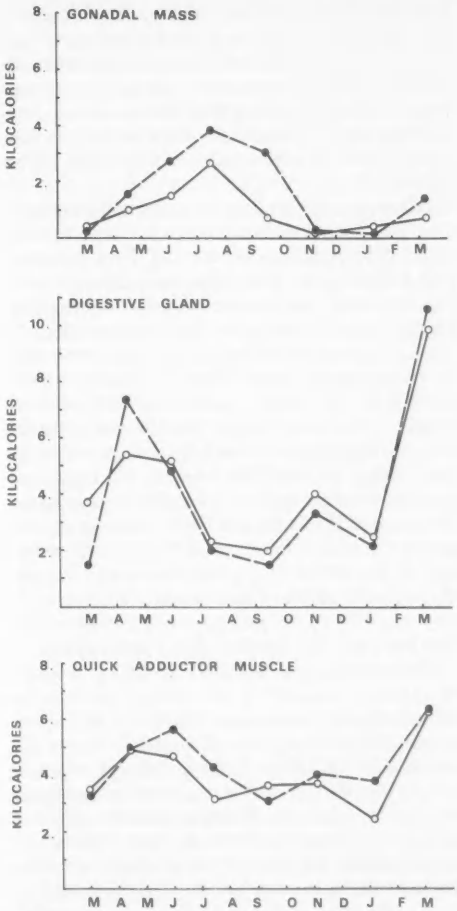

FIGURE 6.—Caloric equivalents (lipid + carbohydrate) for major energy storage tissues of the standard deep-sea scallop (120 mm shell height) over the 1-yr study period. ● = female; ○ = male.

pectinids may occur at times of food shortage (Sastry 1966). Furthermore, neither lipid nor carbohydrate accumulates in the gonad immediately following spawning for use as an overwintering reserve (Thompson 1977; this study).

Histochemical tests do not reveal significant quantities of lipid in either the quick or catch components of the adductor muscle, whereas a substantial amount is detected biochemically. Quantities of sterols (e.g., 22-dehydrocholesterol, cholesterol, brassicasterol, and 24-methylenecholesterol) are present in adductor tissue (Idler et al. 1964) in addition to structural lipids. These high melting point lipids do not color with Oil red *O* and other Sudan dyes (Lillie and Fullmer 1976), and, therefore, cannot be localized histochemically. They are, however, readily extracted by the solvents used for gravimetric lipid analysis. When addressing the problem of distinguishing structural from reserve lipid, Giese (1966) has concluded that lipid levels >5.2% dry weight are reserve. Lipid levels in *P. magellanicus* adductor muscle are never high enough (2.3-4.1%) to meet this criterion.

Neither carbohydrate nor lipid concentrations in the quick component of the adductor muscle were significantly different from those in the catch component in the March and April 1979 samples. Analysis of the catch component was therefore discontinued. De Zwaan et al. (1980), however, found higher concentrations (2.5×) of glycogen in the phasic (= quick) than in the catch adductor of *P. magellanicus* sampled in July at a time when glycogen levels were at a peak. As with our samples, no difference in lipid concentrations was observed. Taken together, these results may indicate that both components of the adductor contain approximately the same carbohydrate levels during the winter and early spring, but that the quick component rapidly overbalances the catch adductor in importance as a site of carbohydrate reserves.

Gametogenesis is intimately related to energy-reserve fluctuations in *P. magellanicus*. In January, while gametogenesis has already reached the early-development stage (Figure 1), body component indices (Figure 2), dry weights (Figure 3), and energy reserves (Figures 4, 5) within the gonad, digestive gland and quick component of the adductor muscle have fallen to their lowest values. The initiation of gametogenesis, characterized by increased numbers of gonial cells and an apparent increase in mitotic activity, is first seen in early winter, at a time when energy reserves are declining. This initiation thus appears to be dependent on the energy reserves accumulated the previous season, although food availability data are not available to substantiate this hypothesis. Following the initiation of gametogenesis, storage products begin to accumulate in the digestive gland, adductor muscle, and gonad in the late winter to early spring (Figure 6). At the same time, gametogenesis proceeds into the middevel-

opment stage and gonad size increases. The accumulation of reserves is almost certainly due to spring phytoplankton blooms. Following this general buildup of energy reserves and continued maturation of gametes, a marked shift in the condition of the digestive gland and adductor muscle occurs. From June through July and probably into August, there is a sharp drop in DGI and QAI (Figure 2), lipid levels in the digestive gland (Figure 4), and carbohydrate in both the digestive gland and quick component of the adductor muscle (Figure 5). During this time, gametes are ripening, GMI values reach their peak and lipid generally reaches its highest level in the gonad. The completion of gametogenesis therefore seems largely dependent on energy reserves which were accumulated earlier in the spring.

Gonadal weight, glycogen, and lipid concentrations are inversely related to the weight and energy reserves of somatic tissues in a variety of other pectinids. In queen scallop, *Chlamys opercularis*, lipid content of body tissues declined as gonadal lipid increased (Taylor and Venn 1979). Similarly, inverse relationships have been shown for adductor and gonadal dry weights in *Pecten maximus* by Comely (1974) and digestive gland and gonadal indices in bay scallop, *Argopecten* (= *Aequipecten*) *irradians*, by Sastry (1966, 1970). Sastry (1966) has proposed however that the reciprocal relationship between index values may indicate that nutrients supplied by feeding might be rapidly utilized for growth and development without prior storage. Thus a decline in DGI would not represent a drop in actual digestive gland wet weight. However, direct evidence for the transfer of some quantity of materials from body tissues to the gonad has been demonstrated in *A. irradians* using ^{14}C-leucine (Sastry and Blake 1971), in *C. hericia* using lipid ^{14}C-labeled *Chlorella* extract (Vassallo 1973) and in other bivalves (vide Gabbott 1975; Sastry 1979).

During the spring and summer, the loss of energy stores from the digestive gland and adductor muscle could not have been due solely to the transfer of these substances to the gonad. From 13 April to 13 July, more calories were lost from the quick adductor and digestive gland (male, −4.75 kcal; female, −6.00 kcal) than were gained by the gonadal mass (male, +1.57 kcal; female, +2.27 kcal). The real energy loss was probably greater than indicated by these calculations, since contributions from the catch component of the adductor and other somatic tissues were not included in the calculations. Metabolic demands, due to warmer water temperatures and the completion of gonadal maturation probably accounted for the remainder of the lost energy reserves. The possibility that these reserves were used entirely for metabolic needs, while gonadal maturation depended solely on food intake, seems remote.

Following spawning, the condition of the digestive gland and adductor muscle improves, as evidenced by the increase in QAI, CAI, digestive gland lipid, and quick adductor carbohydrate. Reserves do not reach or exceed their springtime levels, such as occurs in *P. maximus*, (Comely 1974), *C. opercularis* (Taylor and Venn 1979), and *C. septemradiata* (Ansell 1974) populations from the Clyde Sea area. Postspawned *Placopecten magellanicus* from Georges Bank attain total fat levels as high as those reached during the springtime (Idler et al. 1964) whereas *P. magellanicus* from a southeast Newfoundland population (Thompson 1977) do not show postspawning, autumn increases in either carbohydrate, lipid or dry weight within the gonad, or somatic tissue. The autumn recovery pattern in Boothbay scallops appears to be intermediate between the Georges Bank and Newfoundland populations.

Reproduction is dependent to varying degrees on available food levels and energy reserves in different temperate marine bivalves. In *C. opercularis* (Taylor and Venn 1979) and *Pecten maximus* (Comely 1974) for example, energy reserves are utilized for both the initiation of gametogenesis and for subsequent gonadal growth. Reserves are apparently required for both these activities in the intertidal mussel, *Mytilus edulis*, as well (Gabbott 1975). In other bivalves, however, intake of food is necessary for vitellogenesis and gonadal growth and often for the initiation of gametogenesis. Gonadal growth in *A. irradians* cannot occur without feeding, since reserve material from the digestive gland and other body tissues are not adequate to sustain maturation (Sastry 1966, 1968, 1970). However, reserves within the digestive gland may supplement nutritional intake needed for gonadal proliferation (Sastry and Blake 1971). Similarly, in *Crassostrea gigas* and *C. virginica* (Gabbott 1975), gonadal growth is accompanied both by springtime feeding and decreased glycogen content of the tissues. Gonadal growth however is supported directly by springtime feeding in *Chlamys septemradiata* (Ansell 1974), although gametogenesis begins during the

winter months when food levels are low and energy reserves in the adductor are falling. In the southeast Newfoundland population of *Placopecten magellanicus*, the initial rise in gonadal DNA content preceeds the usual springtime phytoplankton bloom, occurring instead during the period when both gonadal and somatic dry tissue weights are at an ebb (Thompson 1977). The initiation of gonadal growth in this Newfoundland population, however, appears to be dependent on available food. From measurements of seasonal rates of respiration, excretion, consumption, and filtration in *P. magellanicus* from Narragansett Bay, Ehinger[6] has concluded that intake of food is necessary to meet the energy demands of reproduction. In the present study, the initiation of gametogenesis is shown to occur at a time when reserves, dry weights, and index values of the digestive gland, adductor, and gonad are all declining. Gonadal growth however occurs concurrently with an early spring replenishment of energy reserves. Final maturation of the gametes although dependent on the transfer of energy reserves per se, ultimately relies on the springtime availability of food for the buildup of these reserves.

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LITERATURE CITED

ALTOBELLO, M. A., D. A. STOREY, AND J. M. CONRAD.
1977. The Atlantic sea scallop fishery: a descriptive and econometric analysis. Mass. Agric. Exp. Stn. Res. Bull. 643, 80 p.

ANSELL, A. D.
1974. Seasonal changes in biochemical composition of the bivalve *Chlamys septemradiata* from the Clyde Sea area. Mar. Biol. (Berl.) 25:85-99.

BAIRD, F. T., JR.
1953. Observations on the early life history of the giant scallop (*Pecten magellanicus*). Maine Dep. Sea Shore Fish. Res. Bull. 14, 7 p.

COE, W. R.
1945. Development of the reproductive system and variations in sexuality in *Pecten* and other pelecypod mollusks. Trans. Conn. Acad. Arts Sci. 36:673-700.

COMELY, C. A.
1974. Seasonal variations in the flesh weights and biochemical content of the scallop *Pecten maximus* L. in the Clyde Sea area. J. Cons. 35:281-295.

CRISP, D. J.
1971. Energy flow measurements. *In* N. A. Holme and A. D. McIntyre (editors), Methods for the study of marine benthos, p. 197-279. IBP (Int. Biol. Programme) Handb. 16.

CULLINEY, J. L.
1974. Larval development of the giant scallop *Placopecten magellanicus* (Gmelin). Biol. Bull. (Woods Hole) 147: 321-332.

DE ZWAAN, A., R. J. THOMPSON, AND D. R. LIVINGSTONE.
1980. Physiological and biochemical aspects of the valve snap and valve closure responses in the giant scallop *Placopecten magellanicus*. J. Comp. Physiol. 137(Ser. B): 105-114.

DICKIE, L. M.
1955. Fluctuations in abundance of giant scallop, *Placopecten magellanicus* (Gmelin), in the Digby area of the Bay of Fundy. J. Fish. Res. Board Can. 12:797-857.

DREW, G. A.
1906. The habits, anatomy, and embryology of the Giant Scallop, (*Pecten tenuicostatus*, Mighels). Univ. Maine Stud. 6, 71 p.

GABBOTT, P. A.
1975. Storage cycles in marine bivalve molluscs: a hypothesis concerning the relationship between glycogen metabolism and gametogenesis. Proc. Ninth Europ. Mar. Biol. Symp., p. 191-211.

GIESE, A. C.
1966. Lipids in the economy of marine invertebrates. Physiol. Rev. 46:244-298.

GIESE, A. C., M. A. HART, A. M. SMITH, AND M. A. CHEUNG.
1967. Seasonal changes in body component indices and chemical composition in the Pismo clam *Tivela stultorum*. Comp. Biochem. Physiol. 22:549-561.

GIESE, A. C., AND J. S. PEARSE.
1974. Introduction: General principles. *In* A. C. Giese and J. S. Pearse (editors), Reproduction of marine invertebrates, Vol. I, p. 1-49. Acad. Press, N.Y.

HUMASON, G. L.
1972. Animal tissue techniques. 3d ed. W. H. Freeman, San Franc., 641 p.

IDLER, D. R., T. TAMURA, AND T. WAINAI.
1964. Seasonal variations in the sterol, fat and unsaponifiable components of scallop muscle. J. Fish. Res. Board Can. 21:1035-1042.

LILLIE, R. D., AND H. M. FULLMER.
1976. Histopathologic technic and practical histochemistry. 4th ed. McGraw-Hill, N.Y., 942 p.

[6]Ruth E. Ehinger, State of New Jersey Department of Environmental Protection, Trenton, NJ 08625, pers. commun. June 1979.

MERRILL, A. S., AND R. L. EDWARDS.
1976. Observations on mollusks from a navigation buoy with special emphasis on the sea scallop *Placopecten magellanicus*. Nautilus 90:54-61.

NAIDU, K. S.
1970. Reproduction and breeding cycle of the giant scallop *Placopecten magellanicus* (Gmelin) in Port au Port Bay, Newfoundland. Can. J. Zool. 48:1003-1012.

PETERSON, J. E., K. M. STAHL, AND D. L. MEEKER.
1976. Simplified extraction and cleanup for determining organochlorine pesticides in small biological samples. Bull. Environ. Contam. Toxicol. 15:135-139.

POSGAY, J. A.
1957. The range of the sea scallop. Nautilus 71:55-57.

POSGAY, J. A., AND K. D. NORMAN.
1958. An observation on the spawning of the sea scallop, *Placopecten magellanicus* (Gmelin), on Georges Bank. Limnol. Oceanogr. 3:478.

SASTRY, A. N.
1966. Temperature effects in reproduction of the bay scallop, *Aequipecten irradians* Lamarck. Biol. Bull. (Woods Hole) 130:118-134.
1968. The relationships among food, temperature, and gonad development of the bay scallops *Aequipecten irradians* Lamarck. Physiol. Zool. 41:44-53.
1970. Reproductive physiological variation in latitudinally separated populations of the bay scallop, *Aequipecten irradians* Lamarck. Biol. Bull. (Woods Hole) 138:56-65.
1979. Pelecypoda (excluding Ostreidae). *In* A. C. Giese and J. S. Pearse (editors), Reproduction of marine invertebrates, Vol. V, p. 113-292. Acad. Press, N.Y.

SASTRY, A. N., AND N. J. BLAKE.
1971. Regulation of gonad development in the bay scallop, *Aequipecten irradians* Lamarck. Biol. Bull. (Woods Hole) 140:274-283.

SERCHUK, F. M., P. W. WOOD, J. A. POSGAY, AND B. E. BROWN.
1979. Assessment and status of sea scallop (*Placopecten magellanicus*) populations off the northeast coast of the United States. Proc. Natl. Shellfish. Assoc. 69:161-191.

SHIEH, H. S.
1968. The characterization and incorporation of radioactive bases into scallop phospholipids. Comp. Biochem. Physiol. 27:533-541.

STEEDMAN, H. F.
1960. Section cutting in microscopy. Blackwell Sci., Oxf., 172 p.

TAYLOR, A. C., AND T. J. VENN.
1979. Seasonal variation in weight and biochemical composition of the tissues of the queen scallop, *Chlamys opercularis*, from the Clyde Sea area. J. Mar. Biol. Assoc. U.K. 59:605-621.

THOMPSON, R. J.
1977. Blood chemistry, biochemical composition, and the annual reproductive cycle in the giant scallop, *Placopecten magellanicus*, from southeast Newfoundland. J. Fish. Res. Board Can. 34:2104-2116.

VASSALLO, M. T.
1973. Lipid storage and transfer in the scallop *Chlamys hericia* Gould. Comp. Biochem. Physiol. A44:1169-1175.

WILLIAMS, A. J., AND P. L. LUTZ.
1975. The role of the haemolymph in the carbohydrate metabolism of *Carcinus maenas*. J. Mar. Biol. Assoc. U.K. 55:667-670.

EFFECTS OF PHOTOPERIOD AND FEEDING ON DAILY GROWTH PATTERNS IN OTOLITHS OF JUVENILE *TILAPIA NILOTICA*

KUNIAKI TANAKA, YASUO MUGIYA, AND JURO YAMADA[1]

ABSTRACT

Effects of varying photoperiods and feeding times on the formation of daily rings in otoliths of juvenile *Tilapia nilotica* were studied with a scanning electron microscope. Two alternate concentric zones, each different in structure, were distinguished in the acid-etched ground plane: one thin and appearing as a groove (discontinuous zone) and the other thick and with well-developed, needlelike crystals (incremental zone). The number of incremental zones showed a good correlation with the chronological age in days after hatching for at least 28 days. The otolith showed a daily rhythm of growth under a photoperiod of 24 hours (12 light-12 dark). Growth of incremental zones started a few hours after lights-on and stopped or slowed down within a few hours of the following lights-on, during which time the discontinuous zone seemed to be formed. When the light and dark cycle was reversed, the cycle of otolith growth began to change on the second day and accommodated to the new photocondition 6 days after the reversal. A change in length of light and dark phases (18L-6D or 6L-18D) or a shift of feeding time did not affect the time of the discontinuous and incremental zone formation.

Otoliths have been widely used for aging fishes along with other hard tissues such as scales and vertebrae. Determinations of ages of larvae and juvenile fish will yield information on their early life history which is important for analyses of their population dynamics. However, accurate age determinations in terms of months or days have not been possible for young fish up to 1-yr-old until Pannella (1971, 1974) showed the presence of daily rings in otoliths (sagittae) of some temperate as well as tropical species. Brothers et al. (1976), Struhsaker and Uchiyama (1976), Taubert and Coble (1977), Timola (1977), Barkman (1978), and Radtke and Dean (in press) have studied the use of such rings, or daily increments, for determining the age in days of some larval and adult fish in temperate or tropical species. Their results showed good correlations between the number of rings and the ages in days after hatching in larval fish. However, the number of rings was often greater than the age in days in larval fish and less in adult fish, and the difference seemed to vary by species. This shows that otolith daily rings may be formed in the embryonic stage in some fish (Brothers et al. 1976; Radtke and Dean in press) and that the increments may not be formed in old fish by cessation of growth under some environmental conditions (Taubert and Coble 1977).

In order to accurately interpret otolith daily rings for age readings, it is necessary to understand the mechanisms which induce formation of individual rings. Taubert and Coble (1977) suggested that a 24-h light-dark cycle is essential for the formation of the ring pattern in the otolith of *Tilapia mossambica*. The morphological studies by Degens et al. (1969) and Pannella (1971, 1974) showed that the ring pattern of fish otoliths is composed of increments of two alternate light and dark bands: a thick band of well-developed aragonite crystals with their long axis roughly perpendicular to the outer margin of the otoliths and a relatively thin band intersecting the aragonite crystals.

Our study was undertaken to verify the presence of a daily growth rhythm in the otolith of *T. nilotica* and to determine the time of a day at which a new increment is formed. We investigated the effects of various photoperiods and the feeding time on the zone formation cycle of the otolith.

MATERIALS AND METHODS

Juveniles of *T. nilotica* (12-24 mm standard length) were used. They were obtained by natural fertilization and rearing by eight females in our laboratory. Eggs hatched about 4 d after fertilization and the larvae remained in their mothers' mouths for about 10 d. Immediately after leaving the mothers' mouths, the juveniles were trans-

[1]Laboratory of Physiology and Ecology, Faculty of Fisheries, Hokkaido University, Hakodate, Hokkaido 041, Japan.

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ferred to aquaria and used in the experiments. Water temperature was maintained at 27±0.5° C.

Experiments under 24-h Photoperiod

The juveniles were transferred to four 60 l aerated aquaria, each kept under a different photoregime: 12L-12D (light phase, 0800-2000 h), 12L-12D (light phase, 2000-0800 h), 18L-6D (light phase, 0800-0200 h), and 6L-18D (light phase, 0800-1400 h). For lighting, a daylight fluorescent lamp (20 W) was fixed 15 cm above the water surface. In all groups, fish were fed to satiation on fish food pellets supplied throughout the 24-h photoperiods. After acclimation to each condition for at least 12 d, 6-10 fish were killed every 3 h and their otoliths removed for measurement of completion of the newest increment. In addition, 10 fish in the first group (12L-12D, light phase, 0800-2000 h) were killed 19 and 28 d after hatching to compare the number of otolith rings with the fish's age in days.

Feeding Experiments

For experiments on effects of feeding we used two groups of juvenile fish of the same brood. Five days after leaving their mother's mouth, one group was fed for 3 h after each lights-on; and the other group was fed for 3 h before lights-off under 12L-12D cycle (light phase, 1200-2400 h). The experiment lasted 15 d. Five fish were killed from each group every 3 h during the last 2 d of the experiment and otoliths were examined for completeness of the newest increment.

Otolith Preparation for Scanning Electron Microscopy

Otoliths (sagittae) were removed from the fish under a dissecting microscope, washed in water, embedded in a few drops of epoxy resin (Bond E,[2] Konishi Co.), and placed on a glass microscope slide. After hardening, both otoliths from each fish were ground by hand with a whetstone to the mid-transverse plane, parallel to the long or short axis, and then polished with a compound whetting paste for sharpening microtome knives. The specimens were cleaned in xylene, etched with 0.5% HCl for about 20 s, and coated with gold in vacuum. The specimens were examined with a JSM-25 scanning electron microscope (SEM) at 15 kV for number of growth rings or for determination of completeness of the newest increment.

For the observation of the internal structure, otoliths were placed in a drop of water and broken into several pieces by a razor blade. The broken pieces were air-dried, coated with gold, and the nonetched fractured surface was observed with the SEM.

Measurement of Daily Growth Rhythm

In order to determine the exact hour when a new increment is formed in the otolith, we calculated the index of completion for current increment (C) by the following formula:

$$C = \frac{W_n}{W_{n-1}} \times 100$$

where W_n = width of current increment
W_{n-1} = width of previous complete increment.

Measurements were made on SEM photographs of specimens collected every 3 h. Following the change of C in time sequence, one can estimate the time of completion or start of zone formation when C suddenly drops from approximately 100% to a lower level. The area of the measurement of C was at the distal surface near the anterior or the posterior edge of the otolith, where increments are thick, discontinuous, and easily observed.

RESULTS

The sagitta of a juvenile *T. nilotica* takes the form of an oval disc. It lies vertically in the sacculus of the inner ear with its long axis parallel to the anteroposterior axis of the fish. The inner surface of the otolith facing the macula region of the sacculus is somewhat concave, whereas the other surface is slightly convex.

When the otolith is ground parallel to its long or short axis down to the core region, or the growth center, and then etched, it exhibits a concentric ring pattern (Figure 1A), with each ring composed of two alternate layers, each different in structure. One layer usually measures 2-8 μm wide and has needlelike crystals of the aragonite form $CaCO_3$

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

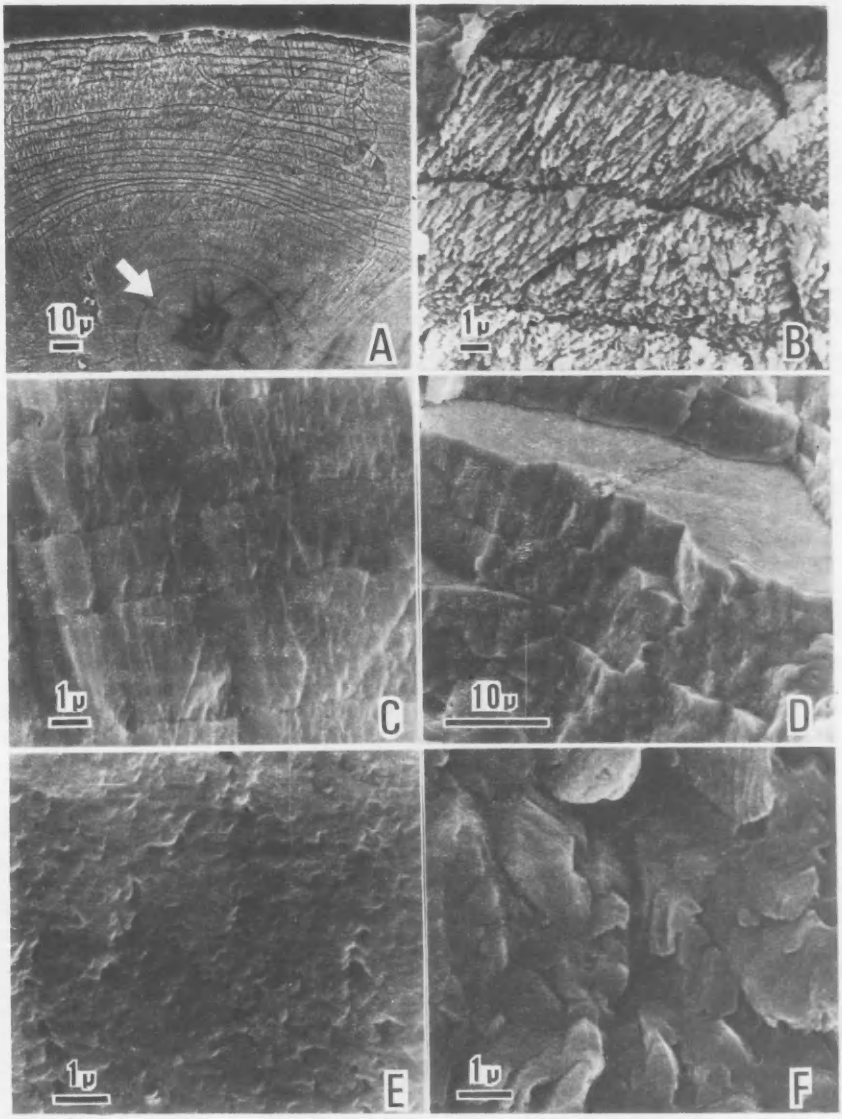

FIGURE 1.—Scanning electron microscope photographs of otoliths of juvenile *Tilapia nilotica*. A) Ground and etched otolith of a fish 28 d after hatching. The core region delimited by the innermost clear discontinuous zone (arrow) shows several vague, narrow bands. The center of the core region is deeply etched and has some spherules. B) Margin of a ground and etched otolith. The outermost incremental zone is not complete. C) Nonetched fracture plane of an otolith. The otolith is composed of a piling up of crystallized lamellae (incremental zone) with thin interstitial layers (discontinuous zone). D) Nonetched fracture plane of an otolith. The surface of a complete crystallized lamella at the boundary of the interstitial layer can be seen. E) Higher magnification of the surface of the crystallized lamella in D. F) Nonetched external surface of an intact otolith to show the growing surface of the outermost incremental zone.

with the long axis nearly perpendicular to the margin of the otolith, while the other is thin (about 0.2-0.5 μm wide) and appears as a concentric groove in slightly etched planes of the otolith (Figure 1B). Most of the grooves are not continuous around the whole area and fade out near the area along the long (anteroposterior) axis of the otolith. Usually, a few grooves in the area around the core region, which is delimited by the earliest clear circular groove, are weakly etched and set at wide intervals (Figure 1A).

On the other hand, examinations of nonetched fracture planes of the otolith revealed several thick crystallized lamellae piled up with narrow (<0.1 μm) interstitial layers between them (Figure 1C, D). The surface of a completed crystallized lamella that was fractured tangentially at the boundary to the interstice was observed to be flat and smooth (Figure 1D, E), while the growing surface of the otolith was rough with stacked crystals (Figure 1F). Therefore, we consider that the concentric grooves in acid-etched planes correspond to the interstitial layers where the growth of crystallized lamella was interrupted. The grooved zone is here defined as the discontinuous zone and the crystallized lamella as the incremental zone, both zones constituting a unit increment.

The core region, defined by the earliest clear discontinuous zone, was about 40 μm in diameter and had several, usually five or more, narrow unclear rings (Figures 1A, 2A). Ten or more spherules of crystals, about 1.5 μm in diameter, were aggregated at the center of the core region. Some of them had the relatively finely organized core surrounded by coarse granules along the margin (Figure 2B). The peripheral region of the aggregate of the spherules was often deeply etched and appeared as a hole.

Correlation between the Number of Otolith Rings and Age in Days after Hatching

The number of rings (incremental zones) was counted from preparations of otoliths from fish 19 and 28 d after hatching. In this case, unclear and narrow rings in the core region were not counted because they seemed to be formed during the embryonic stage. Sixteen otoliths from 8 fish 19 d after hatching and 14 otoliths from 7 fish 28 d after hatching showed 18.89 ± 0.23 and 27.12 ± 0.27 (mean ± SE) rings, respectively. The observed close correlations between the number of rings and the age in chronological days indicated that the ring formation proceeded on a daily basis until at least 28 d after hatching.

Formation of Otolith Rings Under a 12L-12D Photoperiod

When fish were acclimated to a 12L-12D photoperiod of lights-on at 0800 h and lights-off at 2000

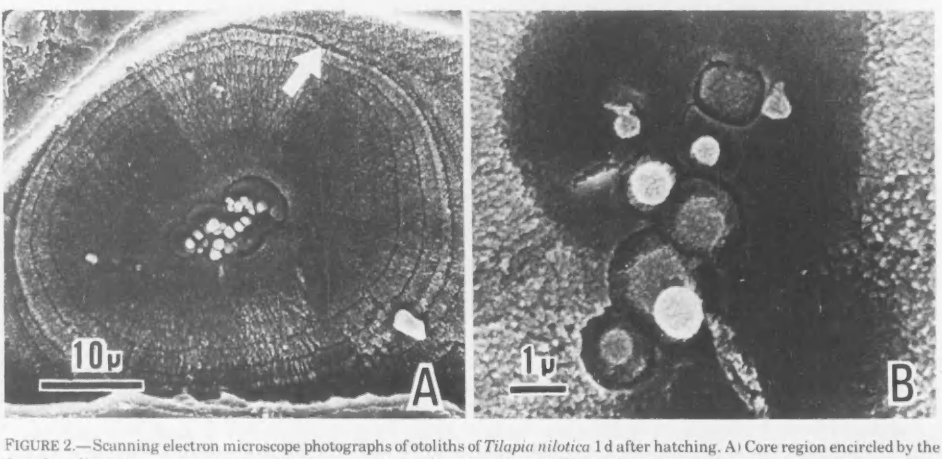

FIGURE 2.—Scanning electron microscope photographs of otoliths of *Tilapia nilotica* 1 d after hatching. A) Core region encircled by the first clear discontinuous zone (arrow). An aggregate of a number of small crystallized spherules is visible in the center. B) Crystallized spherules in the center area of the core region.

h, the otolith showed two phases, growth and rest, in a 24-h period (Figure 3A). The growth phase started between 0900 h and 1200 h and continued until 0500-0800 h next morning. The growth seemed to stop or slow down about the time of lights-on, resulting in the formation of a discontinuous zone. After several hours, the otolith started the next cycle of growth. This growth pattern occurred regularly for a consecutive 3-d period (Figure 3A). Accordingly, one incremental and one discontinuous zone were formed in the otolith in 24 h. When the photoperiod was reversed to lights-on at 2000 h and lights-off at 0800 h, the time of zone formation was also shifted about 12 h (Figure 3B), i.e., the growth phase started at sometime between 2100 h and 2400 h and lasted until about 2100 h. It should be noted that the formation of the incremental zone started a few hours after lights-on in both the experiments.

To see how the time of incremental zone formation shifts following a sudden reversal of light and dark phases (12-h shift), the index of completion for current increment at 2000 h was traced through the reversal (Figure 4). Under the ordinary photoperiod before the change, the index had been maintained at about 50% and persisted in the first day after the shift to the new photoperiod. However, the index at 2000 h became variable in the second day, and then gradually changed to a level of about 100% by the sixth day.

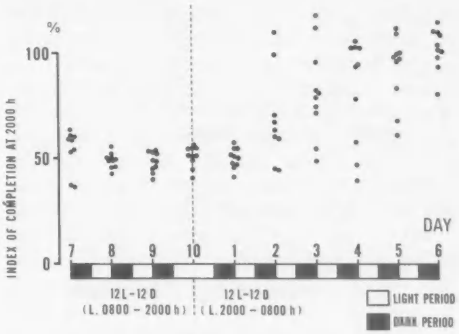

FIGURE 4.—Change in the index of completion for current increment at 2000 h in *Tilapia nilotica* otoliths when the fish were kept under a photoperiod of 12L-12D (light phase, 0800-2000 h) for 10 d and then transferred to the reversed light condition (light phase, 2000-0800 h). Each dot represents one otolith.

Formation of Otolith Rings Under 18L-6D and 6L-18D Photoperiods

The daily growth pattern was found to be the same in the group acclimated to photoperiods of lights-on at 0800 h and lights-off at 0200 h (18L-6D) and in the other with lights-off at 1400 h (6L-18D) despite the 12-h shift in the time of lights-off (Figure 5). The growth phase started about 3 h after lights-on and continued until about 0800 h the following morning. Thus, the discontinuous zones were formed sometime between 0800 h and 1100 h in both groups. It was also observed in both groups that the growth slowed down several hours before lights-on, as seen in 12L-12D experiments.

Feeding Time and the Formation of Otolith Rings

Two groups of fish were acclimated to different feeding schedules under the same photocondition (12L-12D, light phase, 1200-2400 h). One group

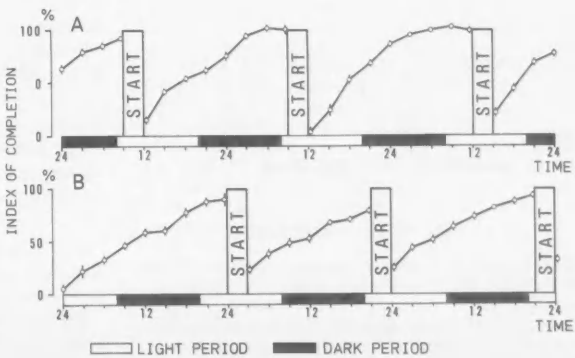

FIGURE 3.—Daily growth of *Tilapia nilotica* otoliths as represented by changes in the index of completion for current increment every 3 h for 72 h. The fish were maintained under two contrasting photoperiods: A) 12L-12D (light phase, 0800-2000 h); B) 12L-12D (light phase, 2000-0800 h). Each circle represents mean ± SE for six fish. START = start of new incremental zone.

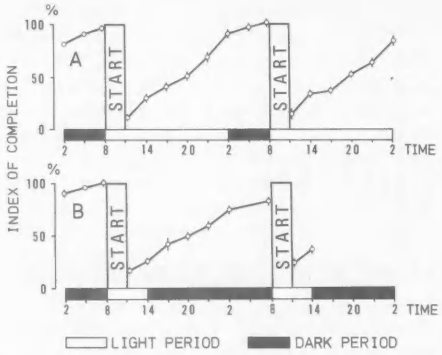

FIGURE 5.—Effects of long and short light periods on the daily growth of *Tilapia nilotica* otoliths. A) 18L-6D, light phase, 0800-0200 h; B) 6L-18D, light phase, 0800-1400 h. Each circle represents mean ± SE for five or six fish. START = start of new incremental zone.

was fed during the first 3 h of light phases while the other was fed during the last 3 h of light phases, giving a 9-h difference in the beginning feeding time. However, no significant difference was found in the time of discontinuous zone formation in both groups (Figure 6). The zone was completed 1 or 2 h after lights-on in both groups, showing that the feeding time had no apparent effect on the formation of otolith rings under the 12L-12D photoperiod.

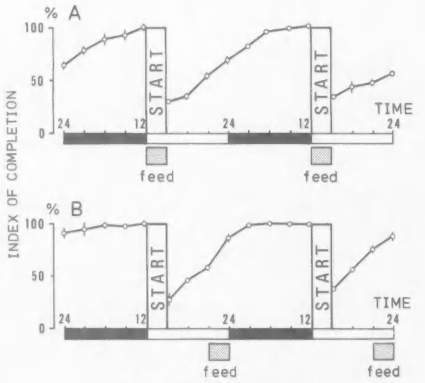

FIGURE 6.—Effects of feeding time on daily growth of *Tilapia nilotica* otoliths when the fish were reared under 12L-12D (light phase, 1200-2400 h). A) fed for 3 h after the onset of light phase; B) fed for 3 h before the end of light phase. Each circle represents mean ± SE for five fish. START = start of new incremental zone.

DISCUSSION

The ground and etched plane of otoliths of *T. nilotica* exhibited a concentric ring pattern of thick incremental and thin discontinuous zones. In other teleost otoliths, a unit increment has been described as composed of light and dark bands in light microscope observations of replicas of ground and etched planes (Pannella 1971, 1974) and light microscope (Struhsaker and Uchiyama 1976; Taubert and Coble 1977; Barkman 1978) or SEM (Pannella 1974; Brothers et al. 1976; Timola 1977) observations of ground and etched specimens. The thickness of each band was variable but not as different as observed with the discontinuous and incremental zones in our results. This may be due to different ways of preparation and observation with different species of different ages. In particular, the thickness of discontinuous zones may vary depending on the concentration of acid and the etching time.

It has been considered that the band easily etched by acid contains more calcium and less organic materials (Brothers et al. 1976; Timola 1977). However, our observations of nonetched fracture planes in comparison with ground and etched planes indicated that acid effects thin interstitial layers between thick crystalline lamellae to form grooves, which are wider than the interstitial layers. This may be interpreted as caused by dissolution of calcium from the interstitial layers, and further, from the crystallized lamellae. The presence of organic materials intersecting growing crystals was reported in otoliths of various fishes (Degens et al. 1969; Pannella 1971). Dunkelberger et al. (1980) showed in a transmission electron microscope study of the *Fundulus* otolith that an interlamellar organic matrix interrupts each growth layer. Therefore, we consider that etching by acid discloses a layer containing more organic materials and less calcium and that acid infiltrated into the layer would affect crystalline layers at both sides. The discontinuous zones in the area along the anteroposterior axis of the otolith were not clear. Also, a few weakly etched discontinuous zones at wide intervals were found near the core region. This shows a possibility that clearness of a discontinuous zone reflects the growth rate of the otolith in relation to the ratio in amount of organic versus inorganic materials.

Results of our experiments in which the completeness of the outermost incremental zone was

measured every 3 h clearly showed that the ring is formed periodically every 24 h. This is supported with the observation that the number of rings (incremental zones), except those in the core region, is in good correlation with the chronological age in days after hatching of the fish. This also shows that the core region is formed during the embryonic stage. Several crystallized spherules found in the center of the core region indicate that the otolith rudiment is formed by fusion of many small primordia. Their presence is helpful to identify the plane that exactly passes through the center of the otolith.

The rate of otolith growth, judged from a change of the completeness of current increment, decreased or stopped for at least a few hours before and/or after the beginning of a light period in all the experiments. This may indicate that the growth of aragonite crystals at the margin of the otolith stopped or slowed down during this period of a day. On the other hand, growth of the otolith was apparent the rest of the time, showing that crystals deposited more rapidly. The structural difference observed between the surface of a complete crystalline layer and the outer surface of the growing otolith, flat and smooth in the former and rough with stacked crystals in the latter, also shows a difference in growth phases. These observations confirmed that in the fast growth phase an incremental zone is formed in the margin of the otolith and in the resting phase a discontinuous zone is formed. In relation to the structure of incremental and discontinuous zones discussed above, a cyclic deposition of organic materials or calcium or both seems to occur according to a daily photoperiod. Recently, Mugiya et al. (1981) reported that ^{45}Ca uptake by goldfish otoliths slowed down or stopped at sunrise and resumed in 3 h.

When a light and dark cycle was suddenly reversed, it took at least 6 d for the rhythm of the otolith growth to be adapted to the new photocondition. This indicates that otolith growth is primarily controlled by an endogenous rhythm synchronized with the environmental photoperiod. Taubert and Coble (1977) also presented a hypothesis that the formation of otolith rings is controlled by an internal, diurnal clock when fish are exposed to a 24-h photoperiod.

It was clearly shown that the otolith resumes its growth a few hours after lights-on, leaving a new discontinuous zone behind it. This pattern of growth was not affected by the change of the lengths of light and dark phases such as 18L-6D and 6L-18D. This shows that the stimulus of lights-on entrains the rhythm of otolith growth to the photoperiods and thus is important for the formation of the otolith rings. The importance of this stimulus as a cue for the ring formation is supported by the experiment in which light and dark phases were reversed, where changes in phase of otolith growth started after the first stimulus of lights-on, but not lights-off, in the reversed cycle (Figure 4).

Since *T. nilotica*, as a typical diurnal fish, begins to feed immediately after lights-on, feeding was also expected to be one of the factors which control the daily rhythm of otolith growth. However, a difference of 6 h in daily feeding did not affect the phase of the rhythm. Therefore, feeding time is not critical for the formation of otolith rings when the fish is exposed to a 24-h photoperiod. Taubert and Coble (1977) also showed that the feeding cycle of 24 h did not cause the formation of daily rings on the otolith of *T. mossambica* held under constant light.

ACKNOWLEDGMENTS

We thank Norimitsu Watabe and John M. Dean, University of South Carolina, for their discussion and advice in preparing the manuscript. This work was supported by a fund from the Japan Society for the Promotion of Science awarded for a cooperative research under the Japan-United States Cooperative Science Program.

LITERATURE CITED

BARKMAN, R. C.
1978. The use of otolith growth rings to age young Atlantic silversides, *Menidia menidia*. Trans. Am. Fish. Soc. 107:790-792.

BROTHERS, E. B., C. P. MATHEWS, AND R. LASKER.
1976. Daily growth increments in otoliths from larval and adult fishes. Fish. Bull., U.S. 74:1-8.

DEGENS, E. T., W. G. DEUSER, AND R. L. HAEDRICH.
1969. Molecular structure and composition of fish otoliths. Mar. Biol. (Berl.) 2:105-113.

DUNKELBERGER, D. G., J. M. DEAN, AND N. WATABE.
1980. The ultrastructure of the otolithic membrane and otolith in the juvenile mummichog, *Fundulus heteroclitus*. J. Morphol. 163:367-377.

MUGIYA, Y., N. WATABE, J. YAMADA, J. M. DEAN, D. G. DUNKELBERGER, AND M. SHIMIZU.
1981. Diurnal rhythm in otolith formation in the goldfish, *Carassius auratus*. Comp. Biochem. Physiol. 68A: 659-662.

PANNELLA, G.
1971. Fish otoliths: daily growth layers and periodical patterns. Science (Wash., D.C.) 173:1124-1127.

1974. Otolith growth patterns: an aid in age determination in temperate and tropical fishes. *In* T. B. Bagenal (editor), International symposium of the aging of fish, p. 28-39. Unwin Brothers, Surrey, Engl.

RADTKE, R. L., AND J. M. DEAN.

In press. Increment formation in the otoliths of embryos, larvae, and juveniles of the mummichog, *Fundulus heteroclitus*. Fish. Bull., U.S.

STRUHSAKER, P., AND J. H. UCHIYAMA.

1976. Age and growth of the nehu, *Stolephorus purpureus*) Pisces: Engraulidae), from the Hawaiian Islands as indicated by daily growth increments of sagittae. Fish. Bull., U.S. 74:9-17.

TAUBERT, B. D., AND D. W. COBLE.

1977. Daily rings in otoliths of three species of *Lepomis* and *Tilapia mossambica*. J. Fish. Res. Board Can. 34:332-340.

TIMOLA, O.

1977. Scanning electron microscope studies on the growth patterns of smelt, *Osmerus eperlanus* (L.), otoliths. Aquilo Ser Zool. 17:57-60.

PREY OF THE STELLER SEA LION, *EUMETOPIAS JUBATUS*, IN THE GULF OF ALASKA

KENNETH W. PITCHER[1]

ABSTRACT

Stomach contents of 250 Steller sea lions, *Eumetopias jubatus*, collected in the Gulf of Alaska consisted by volume of 95.7% fishes, 4.2% cephalopods, <0.1% decapod crustaceans, <0.1% shelled-gastropods, and <0.1% mammals. The 10 top-ranked prey were walleye pollock, *Theragra chalcogramma*; squids, Gonatidae; Pacific herring, *Clupea harengus pallasi*; capelin, *Mallotus villosus*; Pacific cod, *Gadus macrocephalus*; salmon, *Oncorhynchus* spp.; octopus, *Octopus* sp.; sculpins, Cottidae; flatfishes, Pleuronectidae; and rockfishes, Scorpaenidae. Walleye pollock was the predominant prey, composing about 58% of the total volume and occurring in 67% of the stomachs with food. Predation on capelin and salmon appeared to be largely limited to spring and summer when these species were abundant in nearshore waters. Utilization of walleye pollock by sea lions appeared to have increased between 1958-60 and 1975-78, perhaps because of an increase in the relative abundance of walleye pollock. There was nearly complete overlap in the diet of sea lions and the harbor seal, *Phoca vitulina richardsi*. Potential competition may have been ameliorated by differences in distribution, differing diving capabilities, a more diverse diet for harbor seals and use of larger prey by sea lions.

The importance of knowledge of diets of marine mammals has become increasingly apparent with the recent emphasis in offshore oil and gas development and the resulting potential for reduction or change in composition of prey resulting from pollution (Evans and Rice 1974). These data are also needed by both fisheries and marine mammal managers, particularly since recent legislation (The Marine Mammal Protection Act of 1972; United States PL 92-522 and The Fishery Conservation and Management Act of 1976; PL 94-265) requires management based on ecosystem concerns.

Between 1975 and 1978 I studied prey utilization by the Steller sea lion, *Eumetopias jubatus*, in the Gulf of Alaska from Cape Suckling to Sanak Island (Figure 1). This area contains an estimated 110,000 to 140,000 sea lions, 10 breeding rookeries, and a mimimum of 50 hauling areas and is considered to be the center of abundance for the species (Calkins and Pitcher[2]).

Several prior studies of sea lion foods (Imler and Sarber 1947; Mathisen et al. 1962; Thorsteinson and Lensink 1962; Fiscus and Baines 1966), although limited in geographic and seasonal coverage, provide a base for comparisons of prey use over time. Historical records of prey abundance (Pereyra and Ronholt[3]) provide valuable insight into prey utilization. The results of a concurrent study of harbor seal, *Phoca vitulina richardsi*, foods (Pitcher 1980) allowed me to compare prey utilization of these two resident pinnipeds with largely overlapping distributions.

METHODS

Between 1975 and 1978, 250 sea lions were collected by shooting from nearshore waters, rookeries, and hauling areas of the Gulf of Alaska (Table 1). Stomach contents were removed in the field, wrapped in muslin, and preserved in 10% Formalin.[4] In 15 cases, when large amounts of freshly eaten prey occurred, the prey were weighed, identified from external characteristics, and disposed of in the field. Volume (cubic centimeters) and weight (grams) of prey were assumed to be equal in these samples (Fiscus and

[1]Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99502.

[2]Calkins, D. G., and K. W. Pitcher. 1981. Population assessment, ecology and trophic relationships of Steller sea lions in the Gulf of Alaska. Outer Continental Shelf Environmental Assessment Program Final Report. Juneau Project Office, P.O. Box 1808, Juneau, AK 99802.

[3]Pereyra, W. R., and L. L. Ronholt. 1976. Baseline studies of demersal resources of the northern Gulf of Alaska shelf and slope. U.S. Dep. Commer., NOAA Processed Rep. NMFS NWFC, 281 p.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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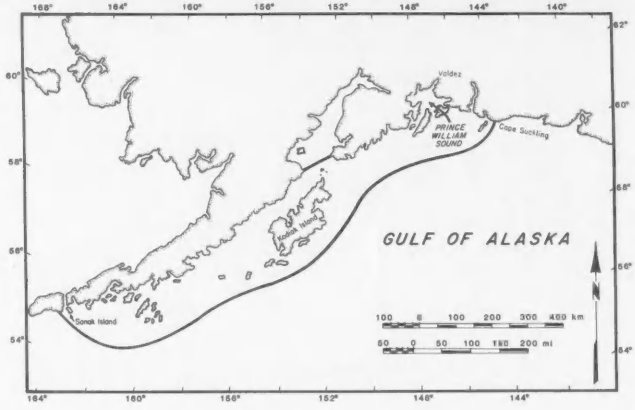

FIGURE 1.—Portion of the Gulf of Alaska where Steller sea lion prey utilization studies were conducted.

TABLE 1.—Comparison of seasonal and geographical distributions of 548 harbor seals and 250 Steller sea lions collected in the Gulf of Alaska. Numbers in the table are percentages of the samples taken during a particular season or in a geographical area.

Species	Winter	Spring	Summer	Fall	Northeastern Gulf of Alaska	Prince William Sound[1]	Kenai	Lower Cook Inlet	Kodiak	Alaska Peninsula
Harbor seals	21.7	44.3	13.3	20.7	5.7	35.8	10.9	6.8	36.7	4.2
Steller sea lions	28.4	35.2	6.0	30.4	4.4	37.2	17.2	0	34.4	6.8

[1]Includes 45 harbor seals from the Copper River Delta.

Baines 1966). For all other samples, volumes and occurrences of the various prey categories were determined in the laboratory. Prey identifications were based primarily on skeletal materials, particularly fish otoliths and cephalopod mandibles (beaks) (Fitch and Brownell 1968; Pinkas et al. 1971). Otoliths and other skeletal components from fish were identified to the lowest taxon possible by comparison with reference materials.

Food habit data were organized and examined as percentage of occurrence (number of stomachs in which a prey item occurred/total number of stomachs with food) and percentage of total volume (total volume of a prey item/total volume of all stomach contents). Confidence intervals for percentages of occurrence were calculated from tables presented by Rohlf and Sokal (1969). In the percent occurrence analysis, unimportant small but numerous organisms may be disproportionately evident (Perrin et al. 1973) as may species which have hard parts which resist digestion (Fiscus and Baines 1966). Volumetric analyses are distorting because various organisms are digested at different rates and because contents are at different stages of digestion when the collections are made (Perrin et al. 1973).

A combination rank index (CRI) was devised to integrate volumetric and occurrence data into a single indicator of prey use. Each prey category was ranked in descending order of percentage of occurrence and percentage of volume. The two rankings for each prey category were multiplied together to produce the CRI.

To compare sizes of walleye pollock, *Theragra chalcogramma*, eaten by Steller sea lions and harbor seals, random samples of walleye pollock otoliths recovered from stomachs were measured (total length). Fork lengths of the fish were then estimated, using a formula derived from regression analysis of otolith length and fish length (Frost and Lowry 1981). Estimated mean fork lengths are given in Table 2.

TABLE 2.—Estimated mean fork lengths based on otolith lengths, of walleye pollock eaten by Steller sea lions and harbor seals.

Item	Sea lions	Harbor seals
Otolith measurements, no.	2,030	2,180
Estimated mean fork length, cm	29.8	19.2
Standard deviation, cm	11.6	9.6
Range, cm	5.6-62.9	4.2-53.2

RESULTS AND DISCUSSION

Prey items were found in 153 of 250 sea lion stomachs examined. Fishes made up 95.7%, cephalopods 4.2%, decapod crustaceans <0.1%, shelled gastropods <0.1%, and mammals <0.1% of the volume of stomach contents (Table 3). Fishes included 14 species representing 11 families. Gadidae composed 59.7% of the total stomach contents and occurred in 82.4% of the stomachs with food. Walleye pollock was by far the dominant prey composing 58.3% of the total volume of stomach contents and occurring in 66.7% of the stomachs with food. Cephalopod remains occurred in 36.6% of stomachs with contents but made up only 4.2% of the total volume of stomach contents. This apparent disparity was probably the result of retention of cephalopod beaks in stomachs (Pitcher 1981) and the volumetric measurement was probably the most accurate measure of importance of cephalopods in the sea lion diet. Invertebrates other than cephalopods were found in 9.2% of the stomachs with food but composed <0.1% of total volume. Remains of two harbor seals were found in one stomach. Major prey were ranked (Table 4) using CRI.

TABLE 3.—Stomach contents of 153 Steller sea lions collected in the Gulf of Alaska.

Prey	Occurrence[1] No.	%[2]	95% C.I.[3]	Volume ml	%[4]
Gastropoda:					
Snails	2	1.3	0.1-4.5	20	<0.1
Cephalopoda	56	36.6	29.5-45.0	15,777	4.2
Octopus, *Octopus* sp.	20	13.1	8.2-19.2	250	<.1
Squids, Gonatidae	35	22.9	16.7-30.4	15,507	4.2
Unidentified cephalopods	1	.7	.1-4.5	20	<.1
Decapoda	11	7.2	3.6-12.2	130	<.1
Shrimps	8	5.2	2.2-9.7	100	<.1
Snow crab, *Chionoecetes* sp.	2	1.3	.1-4.5	20	<.1
Spider crab, *Hyas* sp.	1	.7	.1-4.5	10	<.1
Unidentified invertebrates	1	.7	.1-4.5	10	<.1
Rajidae:					
Skate, *Raja* sp.	1	.7	.1-4.5	960	.3
Clupeidae:					
Pacific herring, *Clupea h. pallasi*	16	10.5	5.8-15.8	76,920	20.6
Salmonidae:					
Salmon, *Oncorhynchus* spp.	6	3.9	1.5-8.4	19,160	5.1
Osmeridae:					
Capelin, *Mallotus villosus*	16	10.5	5.8-15.8	27,755	7.4
Gadidae	126	82.4	75.1-87.6	222,772	59.7
Saffron cod, *Eleginus gracilis*	2	1.3	.1-4.5	815	.2
Pacific cod, *Gadus macrocephalus*	19	12.4	7.4-18.1	3,471	.9
Pacific tomcod, *Microgadus proximus*	1	.7	.1-4.5	820	.2
Walleye pollock, *Theragra chalcogramma*	102	66.7	59.1-74.3	217,746	58.3
Unidentified gadid	2	1.3	.1-4.5	50	<.1
Zoarcidae:					
Eelpout, *Lycodes* sp.	1	.7	.1-4.5	10	<.1
Scorpaenidae:					
Rockfishes, *Sebastes* spp.	4	2.6	1.0-7.1	3,030	.8
Cottidae, sculpins	6	3.9	1.5-8.4	4,960	1.3
Agonidae:					
Sturgeon poacher, *Agonus acipenserinus*	1	.7	.1-4.5	60	<.1
Trichodontidae:					
Pacific sandfish, *Trichodon trichodon*	2	1.3	.1-4.5	300	<.1
Pleuronectidae, flatfishes	7	4.6	2.2-9.7	1,030	.3
Unidentified fishes	4	2.6	1.0-7.1	40	<.1
Harbor seal, *Phoca v. richardsi*	1	.7	.1-4.5	250	<.1
Total volume				373,184	

[1]Number of stomachs in which a prey item occurred.
[2]Number of occurrences/total number of stomachs with food (153).
[3]95% confidence interval.
[4]Total volume of a prey item/total volume of stomach contents.

TABLE 4.—Rankings by combination rank index (CRI, see Methods) of the 10 top-ranked prey of Steller sea lions collected in the Gulf of Alaska.

Rank	CRI	Prey	Percentage occurrence	Percentage volume
1	1	Walleye pollock	66.7	58.3
2	10	Squids	22.9	4.2
3	11	Pacific herring	10.5	20.6
4	16.5	Capelin	10.5	7.4
5	25	Pacific cod	12.4	.9
6	38	Salmon	3.9	5.1
7	51	Octopus	13.1	<.1
8	57	Sculpins	3.9	1.3
9	76	Flatfishes	4.6	.3
10	88	Rockfishes	2.6	.8

Predation on salmon, *Oncorhynchus* spp., and capelin, *Mallotus villosus*, appeared to be largely limited to spring and summer. Salmon occurred in 6 (12%) and capelin in 15 (30%) of 50 stomachs containing food collected from April through September. Salmon was not encountered and capelin was found only once (1%) in 103 stomachs containing food collected from October through March. This likely reflected seasonal, nearshore distribution associated with spawning in these species (Hart 1973; Jangaard 1974). I found a similar seasonal pattern of harbor seal predation on salmon and capelin in the Gulf of Alaska (Pitcher 1980).

Pacific herring, *Clupea harengus pallasi*, and squids were extensively used by sea lions in Prince William Sound but appeared to be relatively unimportant in other areas. Fifteen of 16 stomachs containing Pacific herring and 30 of 35 stomachs containing squids were from Prince William Sound both highly significant deviations (χ^2 = 12.30 and 16.61, $P<0.001$) from expected values based on the distribution of stomachs containing food (73 of 153 were from Prince William Sound). Harbor seals also appeared to utilize more squids and Pacific herring in Prince William Sound than in other areas of the gulf, which was attributed to differing water depths and bottom topography (Pitcher 1980).

Three studies of sea lion foods in which a total of 135 stomachs containing food were examined were conducted in the Gulf of Alaska between 1958 and 1960 (Mathisen et al. 1962; Thorsteinson and Lensink 1962; Fiscus and Baines 1966). Major prey included shelled mollusks; cephalopods; Pacific sand lance, *Ammodytes hexapterus*; rockfishes; and smelts. Because geographic and seasonal composition of these samples and my collections were not strictly comparable (previous collections were nearly all near rookeries during the breeding season, while I sampled throughout much of the year at a wide range of locations) strict comparisons of the data are not possible. However, one major difference was apparent; walleye pollock, the predominant prey in my sample, was not found in the earlier studies. Concurrent with this apparent increase of walleye pollock in the sea lion diet has been an increase in walleye pollock abundance in the Gulf of Alaska. Between 1961 and 1973-75 walleye pollock increased from 5 to 45% by weight of total demersal fish stocks and was found to be the predominant species (Pereyra and Ronholt footnote 3).

One additional collection of seven sea lions was made in 1945 (Imler and Sarber 1947). Walleye pollock and flatfishes were the major foods.

Harbor seals and Steller sea lions are the only abundant pinnipeds resident in nearshore regions of the Gulf of Alaska. Food habit studies of both species were conducted concurrently; both sea lions and harbor seals (Pitcher 1980) frequently were collected on the same trips. This resulted in relatively comparable geographic and seasonal coverage (Table 1). Results of the two studies were similar (Table 5) with nearly complete overlap of principal prey. Spearman rank correlation analysis showed a significant positive correlation (r_s = 0.67, $P<0.01$) between the rankings of principal prey eaten by both sea lions and harbor seals. The percentage of cephalopods eaten by both predators was similar; however, sea lions ate more squids while harbor seals consumed more octopus. Walleye pollock was the top-ranked prey of both sea lions and harbor seals; however, the percentage of occurrence was nearly twice as high for sea lions (66.7%) as for harbor seals (34.9%). Eulachon, *Thaleicthys pacificus*, and Pacific sand lance were both evident components of the harbor seal diet (occurring in 8.2% and 7.1% of the stomachs, respectively) but were not recorded as food of sea lions during this study. Most eulachon occurrences were from harbor seals collected in freshwater and estuarine habitats of the Copper River Delta (Pitcher 1980) where no sea lions occurred.

Although use of prey by sea lions and harbor seals was similar, several factors may have ameliorated potential competition. Mean length of walleye pollock eaten by sea lions was significantly greater (t = 32.4, $P<0.001$) than for those eaten by harbor seals, based on otoliths recovered from stomachs (Table 2). This may indicate a tendency towards use of larger prey by sea lions. Although distribution of the two species often overlaps in the Gulf of Alaska, sea lions range farther offshore (Fiscus et al.[5]). In addition, harbor seals often use freshwater and estuarine habitats rarely used by sea lions in the Gulf of Alaska. Harbor seals can probably stay submerged for considerably longer periods than sea lions (R. Elsner[6]) which may allow them to more efficiently utilize cryptic and solitary prey such as octopus and flatfishes. Although use of principal prey between the two species was similar, harbor seals had a more diverse diet. They preyed upon a minimum of 31 species (Pitcher 1980) compared with 20 for sea lions. Both sea lions and harbor seals appeared to modify their diets according to prey availability. Several lines of evidence led to this hypothesis. Walleye pollock, the predominant prey of sea lions and harbor seals, was the most abundant species of demersal fish in the area. Similar seasonal and geographic variations in the diets of both species were found which probably reflected use of abundant and readily available prey at that time and location. There were apparent changes over time in the relative composition of the sea lion diet (primarily walleye pollock) which appeared to correlate with changes in prey abundance. Also, reports in the literature indicated use of different prey in other geographic regions (Spalding 1964; Fiscus and Baines 1966).

Four of the five, top-ranked prey of both sea lions and harbor seals (Table 5) were off-bottom schooling species. Many of the important prey reported in other studies of Steller sea lion foods also fit into this category and include Pacific herring; smelts;

[5]Fiscus, C. H., H. W. Braham, R. W. Mercer, R. D. Everitt, B. D. Krogman, P. D. McGuire, C. E. Peterson, R. M. Sonntag, and D. E. Withrow. 1976. Seasonal distribution and relative abundance of marine mammals in the Gulf of Alaska. *In* Environmental assessment of the Alaskan Continental Shelf, Vol. 1, p. 19-264. Principal investigators reports for October-December 1976. Environmental Research Laboratories, NOAA, Boulder, Colo.

[6]R. Elsner, Professor of Physiology, Institute of Marine Science, University of Alaska, Fairbanks, AK 99701, pers. commun. January 1980.

TABLE 5.—Comparative frequency of principal prey ($N \geq 4$) of 250 Steller sea lions and 548 harbor seals collected in the Gulf of Alaska between 1973 and 1978.

	Steller sea lion occurrence				Harbor seal occurrence[1]			
Prey	Rank	No.	%	95% C. I.[2]	Rank	No.	%	95% C. I.[2]
Walleye pollock	1	102	66.7	59.1-74.3	1	94	34.9	29.4-40.9
Squid	2	35	22.9	16.7-30.4	8	20	7.4	4.3-10.7
Octopus	3	20	13.1	8.2-19.2	2	77	28.6	23.8-34.7
Pacific cod	4	19	12.4	7.4-18.1	5	28	10.4	6.8-14.1
Pacific herring	5.5	16	10.5	5.8-15.8	4	29	10.8	7.6-15.3
Capelin	5.5	16	10.5	5.8-15.8	3	40	14.9	11.1-19.8
Shrimps	7	8	5.2	2.2-9.7	10	17	6.3	3.6-9.5
Flatfishes	8	7	4.6	2.2-9.7	6	23	8.6	6.0-13.0
Salmon	9.5	6	3.9	1.5-8.4	13	9	3.3	1.4-5.7
Sculpins	9.5	6	3.9	1.5-8.4	11.5	10	3.7	2.1-7.0
Rockfishes	11	4	2.6	1.0-7.1	17	4	1.5	0.2-3.4
Saffron cod	12.5	2	1.3	0.1-4.5	16	5	1.9	0.8-4.4
Pacific sandfish	12.5	2	1.3	0.1-4.5	11.5	10	3.7	2.1-7.0
Pacific tomcod	14.5	1	.7	0.1-4.5	14	7	2.6	1.4-5.7
Eelpouts	14.5	1	.7	0.1-4.5	15	6	2.2	0.8-4.4
Eulachon	16.5	0	.0	0.0-2.4	7	22	8.2	5.2-11.8
Pacific sand lance	16.5	0	.0	0.0-2.4	9	19	7.1	4.3-10.7
Others		16				31		
Stomachs with food		153				269		

[1]Pitcher (1980).
[2]95% confidence interval.

Pacific cod, *Gadus macrocephalus*; Pacific whiting, *Merluccius productus*; walleye pollock; rockfishes; and Pacific sand lance (Imler and Sarber 1947; Spalding 1964; Fiscus and Baines 1966). Use of this prey type may be important in minimizing foraging effort and conserving energy, compared with the energy expenditures of capturing more solitary species (Smith and Gaskin 1974; Pitcher 1980).

ACKNOWLEDGMENTS

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LITERATURE CITED

EVANS, D. R., AND S. D. RICE.
1974. Effects of oil on marine ecosystems: A review for administrators and policy makers. Fish. Bull., U.S. 72:625-638.

FISCUS, C. H., AND G. A. BAINES.
1966. Food and feeding behavior of Steller sea lions and California sea lions. J. Mammal. 47:192-200.

FITCH, J. E., AND R. L. BROWNELL, JR.
1968. Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. J. Fish. Res. Board Can. 25:2561-2574.

FROST, K. J., AND L. F. LOWRY.
1981. Trophic importance of some marine gadids in northern Alaska and their body-otolith relationships. Fish. Bull., U.S. 79:187-192.

HART, J. L.
1973. Pacific fishes of Canada. Fish. Res. Board Can., Bull. 180, 740 p.

IMLER, R. H., AND H. R. SARBER.
1947. Harbor seals and sea lions in Alaska. U.S. Fish Wildl. Serv., Spec. Sci. Rep. 28, 23 p.

JANGAARD, P. M.
1974. The capelin (*Mallotus villosus*) biology, distribution, exploitation, utilization, and composition. Fish. Res. Board Can., Bull. 186, 70 p.

MATHISEN, O. A., R. T. BAADE, AND R. J. LOPP.
1962. Breeding habits, growth and stomach contents of the Steller sea lion in Alaska. J. Mammal. 43:469-477.

PERRIN, W. F., R. R. WARNER, C. H. FISCUS, AND D. B. HOLTS.
1973. Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares*, in mixed-species aggregations. Fish. Bull., U.S. 71:1077-1092.

PINKAS, L., M. S. OLIPHANT, AND I. L. K. IVERSON.
1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Dep. Fish Game, Fish Bull. 152, 105 p.

PITCHER, K. W.
1980. Food of the harbor seal, *Phoca vitulina richardsi*, in the Gulf of Alaska. Fish. Bull., U.S. 78:544-549.
1981. Stomach contents and feces as indicators of harbor seal, *Phoca vitulina*, foods in the Gulf of Alaska. Fish. Bull., U.S. 78:797-798.
ROHLF, F. J., AND R. R. SOKAL.
1969. Statistical tables. W. H. Freeman, San Franc., 253 p.
SMITH, G. J. D., AND D. E. GASKIN.
1974. The diet of harbor porpoises (*Phocoena phocoena* [L.]) in coastal waters of Eastern Canada with special reference to the Bay of Fundy. Can. J. Zool. 52:777-782.
SPALDING, D. J.
1964. Comparative feeding habits of the fur seal, sea lion and harbour seal on the British Columbia coast. Fish. Res. Board Can., Bull. 146, 52 p.
THORSTEINSON, F. V., AND C. J. LENSINK.
1962. Biological observations of Steller sea lions taken during an experimental harvest. J. Wildl. Manage. 26:353-359.

OFFSHORE DISTRIBUTION OF ALEWIFE, *ALOSA PSEUDOHARENGUS*, AND BLUEBACK HERRING, *ALOSA AESTIVALIS*, ALONG THE ATLANTIC COAST

RICHARD J. NEVES[1]

ABSTRACT

This study of the offshore distribution of alewife, *Alosa pseudoharengus*, and blueback herring, *A. aestivalis*, in the Atlantic Ocean was based on catch data collected over the 16-year period 1963-78 during bottom trawl surveys by the National Marine Fisheries Service and its predecessor agency. All catches of the two species were made where bottom water temperatures ranged from 2° to 17° C, and catches were most frequent at bottom temperatures between 4° and 7° C. Most catches of both species were made at stations where depth was less than 100 m. Chi-square analyses indicated that alewives were captured significantly more often than expected in the 56 to 110 m depth stratum and blueback herring in the 27 to 55 m stratum ($P<0.01$). During summer and autumn, all catches of the two species were confined to the region north of latitude 40° north in three general areas: Nantucket Shoals, Georges Bank, and the perimeter of the Gulf of Maine (especially in autumn along the northwestern edge of the gulf). Winter catches were between latitude 40° and 43° north, and spring catches were distributed throughout the continental shelf area between Cape Hatteras, N.C., and Nova Scotia. Previous studies on juveniles, food of adults, and differences in time of capture during National Marine Fisheries Service surveys indicated that these species are vertical migrators, apparently following the diel movements of zooplankton in the water column.

The alewife, *Alosa pseudoharengus*, and blueback herring, *A. aestivalis*, are anadromous clupeids that support substantial commercial fisheries during their spawning runs into rivers along the Atlantic coast. They are sympatric over most of their range and remarkably similar in external appearance; species separation is based primarily on eye size and the color of the abdominal peritoneum (Scott and Crossman 1973). Except for a description of some biological characteristics of these species from catches on Georges Bank (Netzel and Stanek 1966), virtually nothing has been written about the offshore biology or movements of these "river herring" (a term used by commercial fishermen for the two species combined).

The alewife, which ranges from North Carolina to the St. Lawrence River, Canada, spawns in rivers during spring. Spawning runs occur in a chronological south to north progression, from March through May. The significance of specific water temperatures for both upstream migration and spawning has been well documented for anadromous alewife populations (Cooper 1961; Dominy 1971; Saila et al. 1972; Kissil 1974; Richkus 1974; Tyus 1974). Adults migrate upstream and spawn in ponds, lakes, or slow-flowing stretches of rivers at water temperatures between 12° and 16° C (Bigelow and Schroeder 1953). Available evidence indicates that alewives home to their natal rivers to spawn (Belding 1921; Havey 1961; Thunberg 1971). The young remain in freshwater for several months, migrate downstream during summer and autumn, and generally spend 2 to 4 yr at sea, until sexually mature.

The behavioral response of alewives to changes in water temperature has received special research attention since the species invaded the Great Lakes (Colby 1973; Otto et al. 1976). Large, periodic die-offs in the Great Lakes have indicated a failure of this species to adjust completely to lake conditions. Hypotheses to explain these die-offs have alluded to differences between the lacustrine environment and the ancestral ocean, and their effect on the physiology of preadults (Smith 1968; Colby 1971; Stanley and Colby 1971); however, specific information on the marine phase of the alewife's life history is lacking.

The blueback herring ranges from northern Florida to Nova Scotia but is most abundant along the middle and south Atlantic coast. Its freshwa-

[1]Assistant Unit Leader, Virginia Cooperative Fishery Research Unit, 106 Cheatham Hall, VPI & SU, Blacksburg, VA 24061.

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ter life history is similar to that of the alewife, although its biology has not been as rigorously studied (Scherer 1972; Loesch and Lund 1977). Adults appear in rivers about 1 mo later than alewives and spawn over an extended period, at water temperatures between 21° and 24° C (Bigelow and Schroeder 1953). The young leave freshwater during their first year and remain in the ocean for 2 to 5 yr before returning to spawn.

This paper presents information on the offshore distribution and seasonal movements of these river herring, based on cruise and catch data collected during bottom-trawl surveys from 1963 to 1978 by U.S. research vessels between Cape Hatteras, N.C., and Nova Scotia, Canada.

METHODS

The National Marine Fisheries Service (NMFS) and its predecessor agency, the Bureau of Commercial Fisheries, have conducted bottom trawl surveys each autumn since 1963, using the RV *Albatross IV* and the RV *Delaware II*. The survey area, which extended from Nova Scotia to Cape Hatteras out to a depth of 366 m (Figure 1), was stratified into geographical zones based on depth and area. Coastal sampling stations were outside the 27 m depth contour. Middle Atlantic stations between New Jersey and Cape Hatteras were added during autumn 1967. A stratified, random sampling design was used in the surveys; trawl stations were allocated to strata in proportion to stratum area and randomly assigned within strata (Grosslein 1969). A standard No. 36 Yankee bottom trawl with a 1.25 cm stretched mesh cod end liner was towed at each station for 30 min at an average speed of 3.5 kn. Fall surveys were conducted 24 h/d between 3 September and 16 December 1963-78.

Bottom trawl surveys were conducted each spring during 1968-78 by U.S. vessels over the same geographical area (Figure 1). The No. 36 Yankee trawl was used from 1968 to 1972 and a larger No. 41 Yankee trawl from 1973 to 1978. Trawling procedures were the same as during autumn surveys, and stations were sampled between 4 March and 23 May. Spring and fall cruises were each conducted within an 8-wk period. A detailed description of NMFS bottom trawl surveys and survey procedures was provided by Flescher[2] and Grosslein.[3] All spring and autumn surveys and additional cruises during summer and winter are summarized in Table 1.

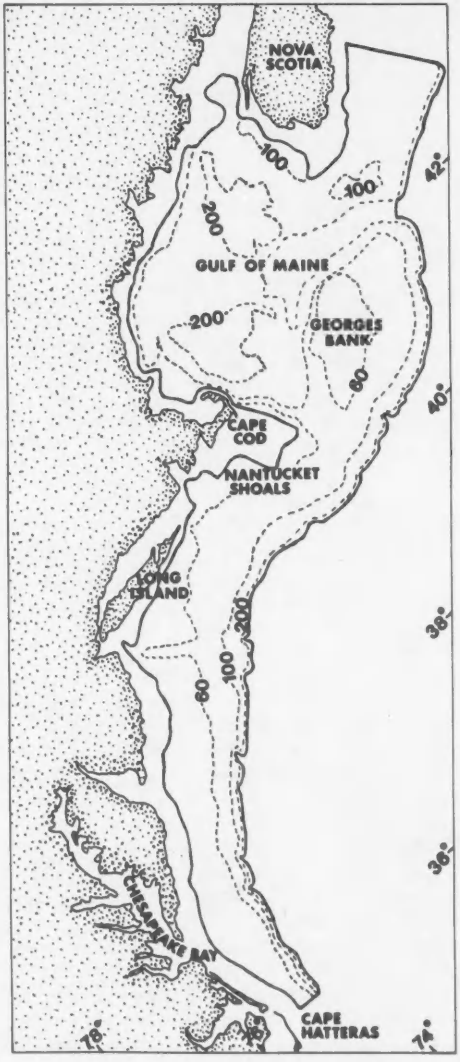

FIGURE 1.—National Marine Fisheries Service bottom trawl survey area, between depths of 27 and 366 m, Cape Hatteras, N.C., to Nova Scotia, western North Atlantic. Contour intervals are in meters (from Neves and Despres 1979).

[2]Flescher, D. 1976. Research vessel cruises, 1963-1975 National Marine Fisheries Service, Woods Hole, Massachusetts. NMFS, Woods Hole, Mass., Lab. Ref. No. 76-14, 30 p.

[3]Grosslein, M. D. 1969. Groundfish survey methods. NMFS, Woods Hole, Mass., Lab. Ref. No. 69-2, 34 p.

TABLE 1.—Summary of seasonal bottom trawl surveys conducted by U.S. research vessels between Cape Hatteras, N.C., and Nova Scotia, 1963-78.

Season	No. of surveys	No. of stations	Inclusive dates
Spring	11	3,097	4 Mar.-23 May
Summer	6	1,137	7 July-31 Aug.
Autumn	16	4,397	3 Sept.-16 Dec.
Winter	3	563	16 Jan.- 8 Apr.
Totals	36	9,194	

Pertinent survey station and catch data included date, location, time, depth, bottom and surface water temperatures, and number and length frequencies of river herring captured. Only catches of 10 or more alewives or blueback herring/trawl tow were used in this study. I plotted catch locations from all surveys (Table 1) by 10′ rectangles of latitude and longitude on depth contour maps according to month or season. Locations of catches during spring (March-May) and autumn (September-November) were plotted by month, although cruise direction and time schedules influenced date of sampling within the survey area. Surveys in summer (June-August) and winter (December-February) were grouped by season because sampling effort and catch frequency were lower during these seasons. Commercial catches reported to the International Commission for the Northwest Atlantic Fisheries (ICNAF[4]) by member nations from 1970 to 1978 were provided by Hodder.[5] These catch data were used to locate U.S. and foreign catches of river herring within each ICNAF division and were correlated with distribution patterns based on survey data. Surface and bottom temperatures (to the nearest 1° C) and depths were plotted for each trawl tow that collected 10 or more alewives or blueback herring.

[4]ICNAF was replaced by the Northwest Atlantic Fisheries Organization (NAFO) in January 1980.

[5]V. M. Hodder, ICNAF Office, Dartmouth, N.S., Canada B2Y 3Y9, pers. commun. July 1977, June 1980.

RESULTS

Bottom trawling at 9,194 stations during the 36 survey cruises yielded 37,313 alewives at 512 stations and 3,058 blueback herring at 96 stations within the survey area. The fish ranged from 6 to 35 cm fork length. Water temperatures recorded at approximately 95% of these collecting stations were used to plot catch frequency at 1° C intervals. Water temperatures at stations where alewives were collected ranged from 2° to 23° C at the surface (Figure 2) and from 3° to 17° C at the bottom (Figure 3). Surface temperatures at stations with blueback herring ranged from 2° to 20° C and

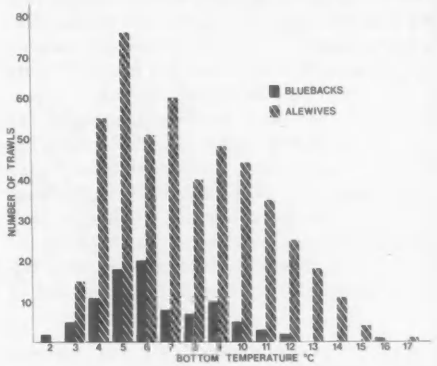

FIGURE 3.—Bottom temperatures at stations where alewives and blueback herring were collected during bottom trawl surveys, 1963-78, Cape Hatteras, N.C., to Nova Scotia.

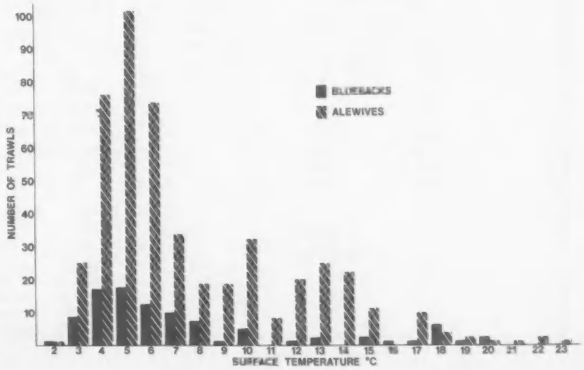

FIGURE 2.—Surface temperatures at stations where alewives and blueback herring were collected during bottom trawl surveys, 1963-78, Cape Hatteras, N.C., to Nova Scotia.

bottom temperatures from 2° to 16° C. Catches of each species were more frequent at stations where both surface and bottom temperatures were 4° to 10° C (Figures 2, 3).

Most stations with bottom temperatures <4° C occurred in the Gulf of Maine during early spring. Stations with bottom temperatures >15° C were mainly off the mid-Atlantic coast during late summer and early autumn. The apparent decline in occurrence of alewives and blueback herring as bottom temperatures increased was examined further by comparing catches with total sampling effort for each bottom temperature (range, 1°-23° C) at which trawls were fished (Table 2). Nearly all blueback herring were taken at water temperatures <13° C. Alewives were caught at temperatures from 3° to 17° C, and frequency of capture was highest at 4° C (Table 2).

Ocean depths at stations where river herring were caught ranged from 20 to 293 m, but most catches of alewives (77%) and blueback herring (83%) were made at stations <100 m deep (Figure 4). Since trawling effort during surveys was proportional to the area of each depth interval, the number of catches within these depth strata was amenable to chi-square analysis with correction for continuity (Zar 1974). A comparison between alewife and blueback herring catches at each depth interval and catches at all other depths combined indicated that both species were collected significantly more often than expected at depths <110 m (Table 3). Based on expected values, blueback herring were captured significantly more often in the 27-55 m depth stratum and alewives in the 56-110 m stratum ($P<0.01$).

TABLE 2.—Total sampling effort and percent of trawl tows with alewives or blueback herring at different bottom temperatures during bottom trawl surveys, 1963-78, Cape Hatteras, N.C., to Nova Scotia.

Bottom temp (° C)	Total trawl tows (no.)	Alewives (%)	Blueback herring (%)
1	9	0	0
2	87	0	2.3
3	243	6.2	2.1
4	589	9.3	1.9
5	1,064	7.1	1.7
6	1,040	4.9	1.9
7	1,018	5.9	.8
8	896	4.5	.8
9	806	6.0	1.2
10	699	6.3	.7
11	653	5.4	.5
12	523	4.8	.4
13	424	4.2	0
14	250	4.4	0
15	153	2.6	0
16	69	0	1.4
17	43	2.3	0
18	31	0	0
19	21	0	0
20	22	0	0
21	21	0	0
22	6	0	0
23	4	0	0

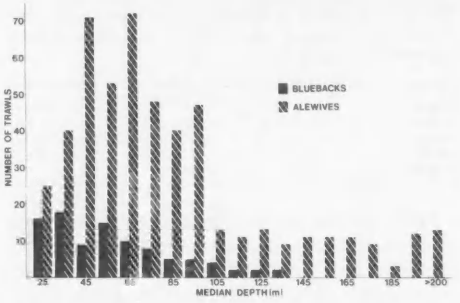

FIGURE 4.—Frequency of catches of alewives and blueback herring in relation to depth at trawling stations, 1963-78, Cape Hatteras, N.C., to Nova Scotia.

Seasonal Distribution

Spring surveys were conducted primarily in March and April, accounting in part for the more frequent collections of alewives and blueback herring during these 2 mo (Figures 5, 6). During the spring, both species were widely distributed along the Middle Atlantic Bight, and mixed catches were common in this region. Alewife catches were also frequent between Cape Cod, Mass., and the western perimeter of Georges Bank (Figure 5). No spring catches of blueback herring were recorded for Georges Bank (Figure 6).

During the summer surveys of July and August, neither species was captured south of lat. 40° N; stations in the central Gulf of Maine were also unproductive (Figure 7). Alewives were collected most frequently on Georges Bank and south of

TABLE 3.—Depth intervals within the survey area and associated catches of alewives (A) and blueback herring (B) during complete bottom trawl surveys, 1967-78, Cape Hatteras, N.C., to Nova Scotia.

Depth interval (m)	Study area		Number of trawl tows with alewives or blueback herring					
			Observed		Expected		χ^2	
	km²	%	A	B	A	B	A	B
27-55	47,412	25.4	120	50	102	22	4.02	46.00**
56-110	55,009	29.5	194	33	118	26	68.45**	2.31
111-185	53,789	28.9	63	4	116	25	33.43**	23.59**
186-366	30,181	16.2	24	0	65	14	30.11**	15.52**
Totals	186,391	100.0	401	87	401	87		

**$P<0.01$.

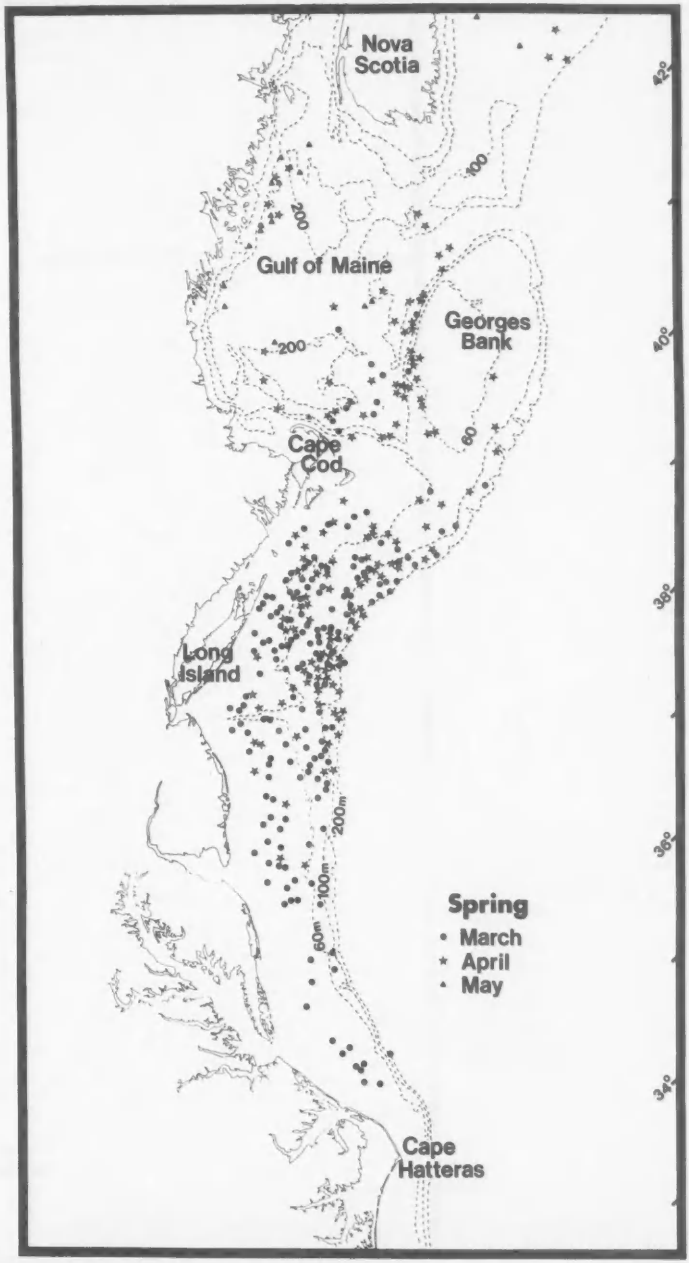

FIGURE 5.—Location of alewife catches during spring bottom trawl surveys, 1968-78, Cape Hatteras, N.C., to Nova Scotia.

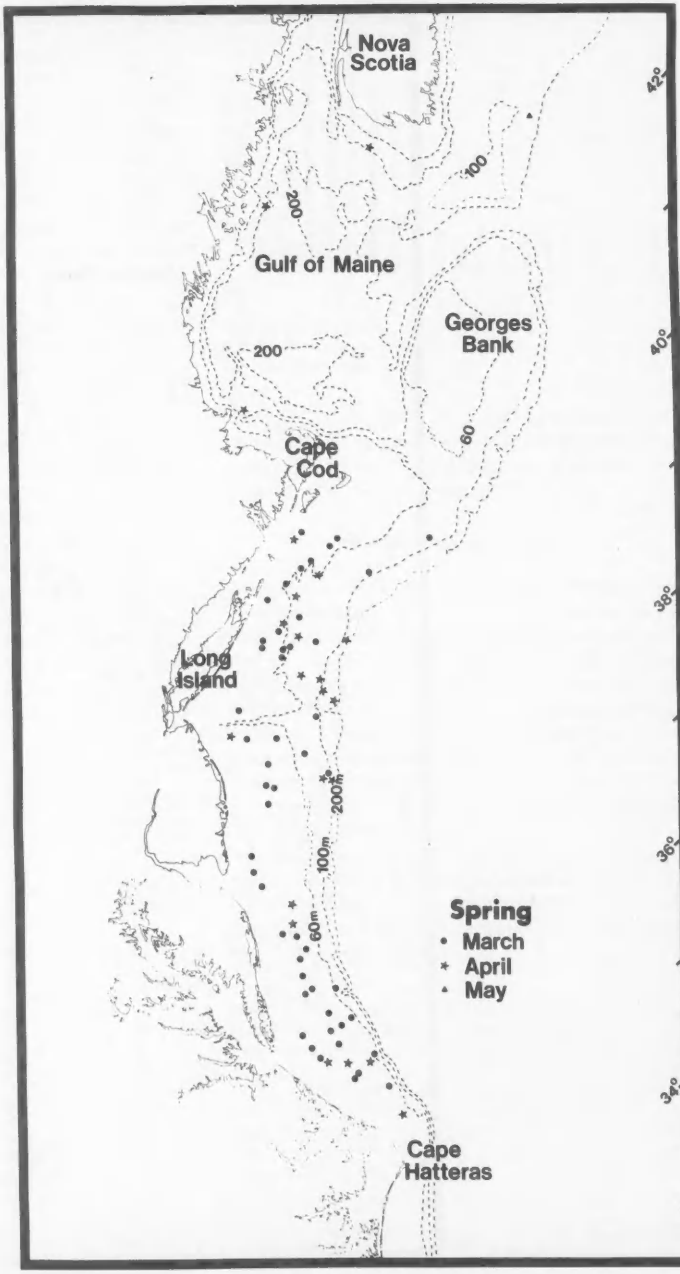

FIGURE 6.—Location of blueback herring catches during spring bottom trawl surveys, 1968-78, Cape Hatteras, N.C., to Nova Scotia.

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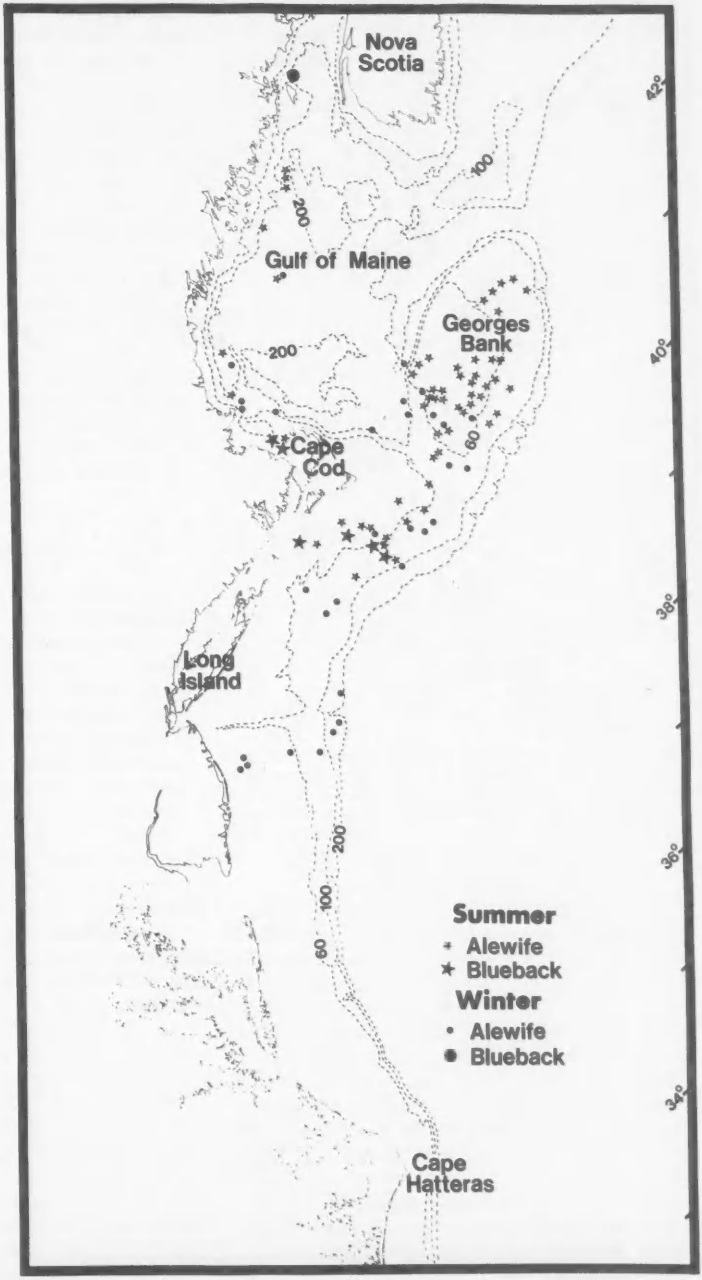

FIGURE 7.—Location of catches of alewives and blueback herring during summer and winter bottom trawl surveys, 1963-78, Cape Hatteras, N.C., to Nova Scotia.

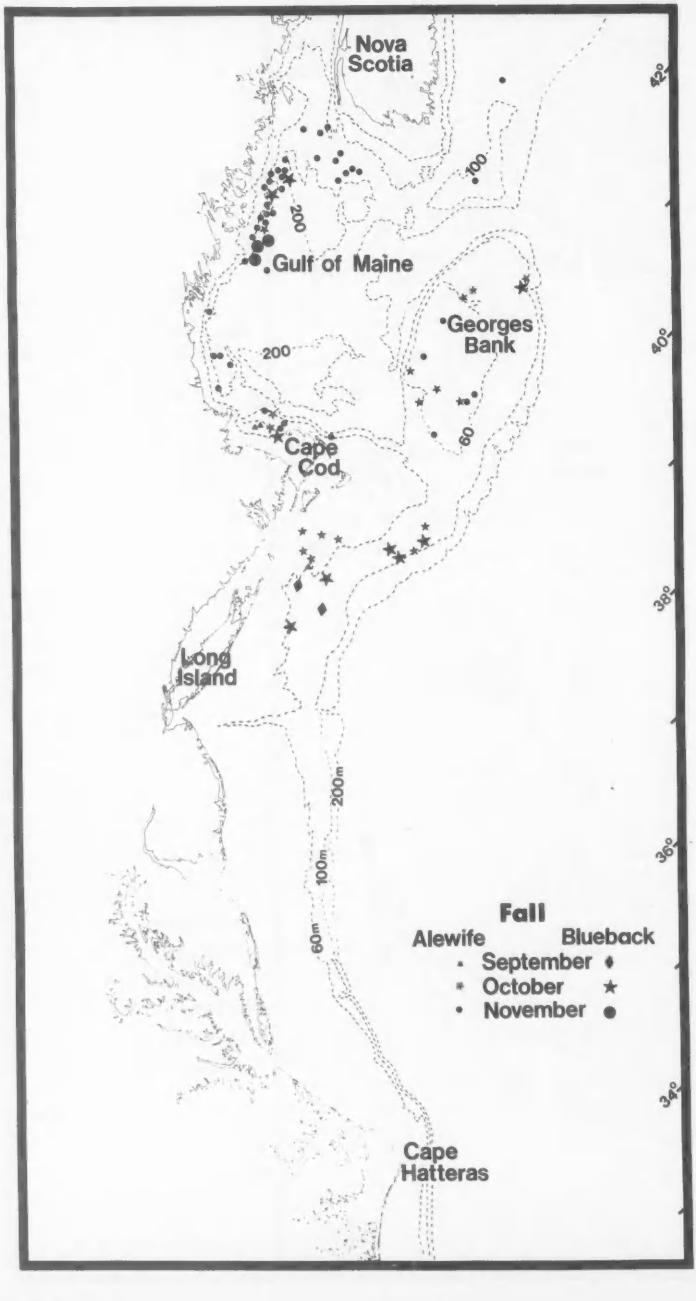

FIGURE 8.—Location of catches of alewives and blueback herring during fall bottom trawl surveys, 1963-78, Cape Hatteras, N.C., to Nova Scotia.

Nantucket Shoals; catch records of blueback herring were too infrequent to determine summer occurrence. Both species were rarely captured in water deeper than 100 m in summer.

During fall surveys, catches of river herring were less frequent than during the spring, even though more stations were sampled (Table 1). Distribution of catches was similar to that in summer, except that a concentration of both species was evident along the northwest perimeter of the Gulf of Maine (Figure 8). Catches of river herring were recorded at most stations in this region. In 12 yr of autumn bottom trawl surveys along the Atlantic coast, river herring were never collected offshore south of lat. 40° N.

The relatively small number of winter sampling stations was inadequate to define the wintering area for either species (Figure 7). The few winter catches were widely distributed, primarily from lat. 40° N (south of Long Island) to lat. 43° N (north of Cape Cod).

Commercial Catches

The time periods for major catches of river herring in ICNAF divisions by domestic (primarily inshore) and foreign (offshore) fisheries are summarized in Figure 9. Domestic catches in Subarea 5 resulted from both inshore and offshore fishing operations. The south to north progression in spawning runs is reflected in the time and location of commercial catches by the United States (Subareas 6 and 5) and Canada (Subarea 4), since most domestic catches occur during the upstream migration of anadromous stocks in each subdivision. The periods of principal foreign catches preceded or overlapped those of domestic catches in coastal waters. The year-round occurrence of river herring between Long Island and Georges Bank, as indicated by NMFS survey data, was corroborated by commercial catches in ICNAF divisions 5Zw and 5Ze (Figure 9).

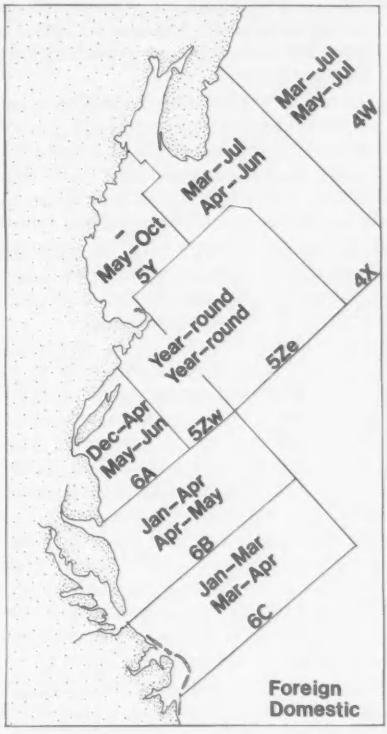

FIGURE 9.—Seasonal distribution of major catches of alewives and blueback herring in divisions of the International Commission for the Northwest Atlantic Fisheries, 1970-78, Cape Hatteras, N.C., to Nova Scotia. Within each division, the months for major catches are shown separately for foreign vessels (upper entry) and the domestic fishery (lower entry).

DISCUSSION

Offshore Distribution

Fish sampling during NMFS bottom trawl surveys covers a large area in a relatively short period and provides the most detailed, available records on offshore distribution of fishes and concurrent environmental conditions. As judged by the accumulated survey data, the seasonal offshore distribution of alewives and blueback herring resembles that of American shad, *Alosa sapidissima* (Neves and Despres 1979). River herring are widely distributed along the Middle Atlantic Bight during spring, appear to move north in the Nantucket Shoals, Georges Bank, and coastal Gulf of Maine areas during summer and early autumn, and then return south to the mid-Atlantic coast in winter and early spring. The extent of overwintering in deep water off the continental shelf is unknown. The similarities in seasonal distribution between American shad and river herring may be indicative of similar inshore and offshore migratory patterns. However, a determination of stock mixing and migratory routes is not possible, because no tagging studies have been conducted

comparable with those on other anadromous species (Merriman 1941; Raney et al. 1954; Talbot and Sykes 1958; Chapoton and Sykes 1961; Leggett and Whitney 1972).

If the water temperature regime recorded for oceanic occurrence of alewives and blueback herring (Figure 3) applies to all stocks of these species at sea, the migratory route of blueback herring populations returning to South Atlantic rivers would be similar to that proposed for American shad by Neves and Despres (1979). Prespawning adults returning to coastal waters from the ocean would encounter a thermal barrier south of Cape Hatteras, where offshore temperatures remain above 17.5° C throughout the year. Migration toward shore north of Cape Hatteras and then south along the coast would appear to be essential for successful homing to South Atlantic rivers.

A determination of oceanic location and migratory routes of river herring stocks has particular relevance to the commercial fishery, centered primarily in Virginia and North Carolina. Large catches of river herring were taken offshore by foreign fishing vessels in ICNAF Subarea 6 during the mid-1960's, and by 1969 foreign catches exceeded domestic catches (McHugh and Ginter 1978). The increase in high-seas catches, consisting of juveniles and adults, was accompanied by a marked decrease in inshore landings. This foreign fishing pressure, added to that of the domestic fishery, resulted in a drastic reduction of total annual catches (Table 4). Street and Davis[6] postulated that this decline reflected a reduction in stock size due to excessive harvest. The United States obtained certain limitations on foreign catches of river herring through bilateral negotiations during the mid-1970's, and after the implementation of the Fishery Conservation and Management Act of 1976 (PL 94-265), offshore catches of river herring by foreign vessels were virtually eliminated. Johnson et al.[7] reported that Virginia landings of river herring in 1978 increased 53% compared with those in 1977, but did not attribute this increase to good recruitment. River herring catches in North Carolina have continued to decline, and water quality degradation in several spawning areas may be creating additional problems (Street[8]). Future monitoring of stock abundance by coastal states should help resolve the question of whether stocks were seriously reduced by offshore fishing.

[6]Street, M. W., and J. Davis. 1976. Notes on the river herring fishery of SA6. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1976, Res. Doc. 76/VI/61, Serial No. 3848, 7 p.

TABLE 4.—Annual catches (metric tons round, fresh) of alewives and blueback herring (species combined) by domestic and foreign fisheries in three ICNAF subareas, 1966-78.

Year	ICNAF subarea 4	5	6	Total
1966	3,703	4,344	21,178	29,225
1967	2,978	9,285	23,182	35,445
1968	3,028	22,598	24,724	50,350
1969	1,655	26,185	34,732	62,572
1970	3,288	14,598	20,842	38,728
1971	10,938	14,618	21,213	46,769
1972	7,948	8,656	5,146	21,750
1973	8,859	5,865	11,202	25,926
1974	17,954	3,771	12,583	34,308
1975	5,683	5,019	9,553	20,255
1976	7,954	1,812	6,444	16,210
1977	7,744	1,765	4,586	14,095
1978	7,626	1,640	4,122	13,388

Depth Distribution

Frequency of alewife and blueback herring catches within the four depth strata indicated that these species occur primarily at water depths <110 m at sea. Both species are size-selective zooplankton feeders (Bigelow and Schroeder 1953; Hildebrand 1963; Brooks and Dodson 1965). My examination of the stomachs of 100 alewives and 75 blueback herring, collected in April 1978 during the spring survey, revealed calanoid copepods, mysids, and other zooplankters in that order of frequency and abundance in both species. The occurrence of major zooplankton concentrations in the Gulf of Maine at depths <100 m (Bigelow 1926; Whiteley 1948) may therefore influence the depth distribution of river herring.

The numerous catches of river herring in the northwestern Gulf of Maine during autumn were centered at about lat. 44° N, long. 68° W. Mean depth at these stations was 112 m (range, 64-179 m), and mean bottom temperature was 9.5° C (range, 8.0°-13.4° C). This apparent concentration of river herring is noteworthy, particularly since studies on zooplankton availability in this region are contradictory. From late summer to December, zooplankton is most abundant in the northern Gulf of Maine (Cohen[9]); however, Sherman (1970)

[7]Johnson, H. B., D. W. Crocker, B. F. Holland, Jr., J. W. Gilliken, D. L. Taylor, and M. W. Street. 1978. Biology and management of mid-Atlantic anadromous fishes under extended jurisdiction. Annu. Rep. Anadromous Fish Proj. 1978, N.C.-Va. AFCS 9-2, 175 p.

[8]M. W. Street, N.C. Div. Mar. Fish. Morehead City, N.C. 28556, pers. commun. June 1980.

[9]Cohen, E. B. 1975. An overview of the plankton communities of the Gulf of Maine. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1975, Res. Doc. No. 106, Ser. No. 3599, 16 p.

recorded low volumes of zooplankton along the northern coast of Maine. Confirmation of river herring abundance in this region requires more extensive investigation.

The apparent difference in preferred depth distribution between the alewife and blueback herring (Table 3) may be related to the diagnostic character differences between these two species. The alewife has a slightly larger eye, an adaptation usually associated with an existence at greater depths (Marshall 1966). In addition, green wavelengths (ca. 500 mμ) penetrate waters of the continental shelf most effectively (Wald et al. 1957). Could the color of the dorsum, green in the alewife and blue in the blueback, be a countershading mechanism for reduced predation within the depth ranges most frequently occupied by each species? No direct evidence is available to support either the eye size or dorsal coloration postulates; however, the vertical segregation evidenced at sea has also been reported for juveniles in rivers (Loesch and Kriete[10]). Juvenile blueback herring occur in the upper levels of the river water column, and juvenile alewives frequent midwater depths.

Diel differences in catchability of river herring were examined by partitioning capture time (eastern standard time) during survey cruises (24 h/d) into day (0600-1800 h) and night (1800-0600 h). Chi-square analysis with correction for continuity on time of capture revealed that catches were made significantly more often ($P<0.01$) during the day than at night (Table 5). Alewives and blueback herring were apparently closer to the bottom during daylight, and thus more susceptible to bottom trawling gear. This diel difference in depth distribution has also been reported for juvenile river herring in estuaries (Warriner et al. 1969; Loesch et al.[11]) and adult alewives in the Great Lakes (Janssen and Brandt 1980).

I deduce from the above observations that river herring are vertical migrators like other schooling clupeids such as American shad and sea herring, *Clupea harengus* (Blaxter 1975; Neves and Despres 1979), which follow the diel movements of zooplankton in the water column. This reliance on zooplankton for food may partly account for the disjunct distribution of river herring in offshore waters during most seasons. Zooplankton distribution in the Gulf of Maine during summer and autumn is closely related to local and regional hydrography (Redfield 1941; Sherman 1970; Cohen footnote 9), and concentrations generally are along areas of current convergence and divergence (Zinkevich 1967). The waters around Georges Bank during the winter are nearly devoid of zooplankton, whereas sizeable neritic populations occur from Nantucket Shoals to southern Long Island (Clarke 1940; Grice and Hart 1962; Zinkevich 1967). Sette (1950) concluded that water temperature had a limiting rather than causal influence on the seasonal movements of the planktivorous Atlantic mackerel, *Scomber scombrus*. Similarly, Neves and Despres (1979) related American shad distribution to bottom temperatures and possibly seasonal shifts in zooplankton concentrations. Catches of river herring in specific areas along Georges Bank, the perimeter of the Gulf of Maine, and south of Nantucket Shoals may therefore be related to zooplankton abundance in these regions, although direct evidence is lacking.

TABLE 5.—Chi-square test comparing the number of day and night catches of alewives (A) and blueback herring (B) during U.S. bottom trawl surveys, 1963-78, Cape Hatteras, N.C., to Nova Scotia.

	Observed		Expected		χ^2	
Time	A	B	A	B	A	B
Day, 0600-1800 h	317	68	250	48		
Night, 1800-0600 h	183	28	250	48		
Total	500	96	500	96	35.4**	15.8**

**$P<0.01$.

Critical data on the oceanic life history of most anadromous fishes are lacking, and my synthesis of NMFS survey data and previous studies on the alewife and blueback herring should be considered tentative. Unanswered questions such as stock identification and mixing, and time and direction of migrations at sea during the year must await prescribed oceanic research.

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[10]Loesch, J. G., and W. H. Kriete, Jr. 1976. Biology and management of river herring and shad. Completion Rep. Anadromous Fish Proj. 1974-1976, Va. AFC 8-1 to 8-3, 226 p.

[11]Loesch, J. G., W. H. Kriete, Jr., H. B. Johnson, B. F. Holland, and M. W. Street. 1977. Biology and management of mid-Atlantic anadromous fishes under extended jurisdiction. Annu. Rep. Anadromous Fish Proj. 1977, N.C.-Va. AFCS 9-1, 183 p.

analysis, and reviewing the manuscript. The Virginia Cooperative Fishery Research Unit provided financial support.

LITERATURE CITED

BELDING, D. L.
1921. A report upon the alewife fisheries of Massachusetts. Mass. Div. Mar. Fish. Contrib. 11, 135 p.

BIGELOW, H. B.
1926. Plankton of the offshore waters of the Gulf of Maine. Bull. U.S. Bur. Fish. 40(2):1-509.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish. Wildl. Serv., Fish Bull. 53, 577 p.

BLAXTER, J. H. S.
1975. The role of light in the vertical migration of fish—a review. *In* G. C. Evans, R. Bainbridge, and O. Rackham (editors), Light as an ecological factor: II, p. 189-210. 16th Symp. Br. Ecol. Soc.

BROOKS, J. L., AND S. I. DODSON.
1965. Predation, body size, and composition of plankton. Science (Wash., D.C.) 150:28-35.

CHAPOTON, R. B., AND J. E. SYKES.
1961. Atlantic coast migration of large striped bass as evidenced by fisheries and tagging. Trans. Am. Fish. Soc. 90:13-20.

CLARKE, G. L.
1940. Comparative richness of zooplankton in coastal and offshore areas of the Atlantic. Biol. Bull. (Woods Hole) 78:226-255.

COLBY, P. J.
1971. Alewife dieoffs: why do they occur? Limnos 4(2):18-27.
1973. Response of the alewives, *Alosa pseudoharengus*, to environmental change. *In* W. Chavin (editor), Responses of fish to environmental changes, p. 163-196. Charles Thomas Publ., Springfield.

COOPER, R. A.
1961. Early life history and spawning migration of the alewife, *Alosa pseudoharengus*. M.S. Thesis, Univ. Rhode Island, Kingston, 58 p.

DOMINY, C. L.
1971. Changes in blood lactic acid concentrations in alewives (*Alosa pseudoharengus*) during passage through a pool and weir fishway. J. Fish. Res. Board Can. 28:1215-1217.

GRICE, G. D., AND A. D. HART.
1962. The abundance, seasonal occurrence and distribution of the epizooplankton between New York and Bermuda. Ecol. Monogr. 32:287-309.

GROSSLEIN, M. D.
1969. Groundfish survey program of BCF Woods Hole. Commer. Fish. Rev. 31(8-9):22-35.

HAVEY, K. A.
1961. Restoration of anadromous alewives at Long Pond, Maine. Trans. Am. Fish. Soc. 90:281-286.

HILDEBRAND, S. F.
1963. *Family* Clupeidae. *In* Y. H. Olsen (editor), Fishes of the western North Atlantic. Part three, p. 257-454. Mem. Sears Found. Mar. Res., Yale Univ. 1.

JANSSEN, J., AND S. B. BRANDT.
1980. Feeding ecology and vertical migration of adult alewives (*Alosa pseudoharengus*) in Lake Michigan. Can. J. Fish. Aquat. Sci. 37:177-184.

KISSIL, G. W.
1974. Spawning of the anadromous alewife, *Alosa pseudoharengus*, in Bride Lake, Connecticut. Trans. Am. Fish. Soc. 103:312-317.

LEGGETT, W. C., AND R. R. WHITNEY.
1972. Water temperature and the migrations of American shad. Fish. Bull., U.S. 70:659-670.

LOESCH, J. G., AND W. A. LUND, JR.
1977. A contribution to the life history of the blueback herring, *Alosa aestivalis*. Trans. Am. Fish. Soc. 106:583-589.

MARSHALL, N. B.
1966. The life of fishes. World Publ. Co., N.Y., 402 p.

MCHUGH, J. L., AND J. J. C. GINTER.
1978. Fisheries. MESA New York Bight Atlas monograph 16. N.Y. Sea Grant Inst., Albany.

MERRIMAN, D.
1941. Studies on the striped bass (*Roccus saxatilis*) of the Atlantic Coast. U.S. Fish Wildl. Serv., Fish. Bull. 50:1-77.

NETZEL, J., AND E. STANEK.
1966. Some biological characteristics of blueback, *Pomolobus aestivalis* (Mitch.), and alewife, *Pomolobus pseudoharengus* (Wils.), from Georges Bank, July and October, 1964. Int. Comm. Northwest Atl. Fish., Res. Bull. 3, 5 p.

NEVES, R. J., AND L. DESPRES.
1979. The oceanic migration of American shad, *Alosa sapidissima*, along the Atlantic coast. Fish. Bull., U.S. 77:199-212.

OTTO, R. G., M. A. KITCHEL, AND J. O'HARA RICE.
1976. Lethal and preferred temperatures of the alewife (*Alosa pseudoharengus*) in Lake Michigan. Trans. Am. Fish. Soc. 105:96-106.

RANEY, E. C., W. S. WOOLCOTT, AND A. G. MEHRING.
1954. Migratory pattern and racial structure of Atlantic coast striped bass. Trans. N. Am. Wildl. Nat. Resour. Conf. 19:376-396.

REDFIELD, A. C.
1941. The effect of the circulation of water on the distribution of the calanoid community in the Gulf of Maine. Biol. Bull. (Woods Hole) 80:86-110.

RICHKUS, W. A.
1974. Factors influencing the seasonal and daily patterns of alewife (*Alosa pseudoharengus*) migration in a Rhode Island river. J. Fish. Res. Board Can. 31:1485-1497.

SAILA, S. B., T. T. POLGAR, D. J. SHEEHY, AND J. M. FLOWERS.
1972. Correlations between alewife activity and environmental variables at a fishway. Trans. Am. Fish. Soc. 101:583-594.

SCHERER, M. D.
1972. The biology of the blueback herring (*Alosa aestivalis* Mitchill) in the Connecticut River above the Holyoke Dam, Holyoke, Massachusetts. M.S. Thesis, Univ. Massachusetts, Amherst, 90 p.

SCOTT, W. B., AND E. J. CROSSMAN.
1973. Freshwater fishes of Canada. Fish. Res. Board Can., Bull. 184, 966 p.

SETTE, O. E.
1950. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part II. Migrations and habits. U.S. Fish Wildl. Serv., Fish. Bull. 51:251-358.

SHERMAN, K.
1970. Seasonal and areal distribution of zooplankton in coastal waters of the Gulf of Maine, 1967 and 1968. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 594, 6 p.

SMITH, S. H.
1968. That little pest, the alewife. Limnos 1(2):12-20.

STANLEY, J. G., AND P. J. COLBY.
1971. Effects of temperature on electrolyte balance and osmoregulation in the alewife (*Alosa pseudoharengus*) in fresh and sea water. Trans. Am. Fish. Soc. 100:624-638.

TALBOT, G. B., AND J. E. SYKES.
1958. Atlantic coast migrations of American shad. U.S. Fish Wildl. Serv., Fish. Bull. 58:473-490.

THUNBERG, B. E.
1971. Olfaction in parent stream selection by the alewife (*Alosa pseudoharengus*). Anim. Behav. 19:217-225.

TYUS, H. M.
1974. Movements and spawning of anadromous alewives, *Alosa pseudoharengus* (Wilson) at Lake Mattamuskeet, North Carolina. Trans. Am. Fish. Soc. 103:392-396.

WALD, G., P. K. BROWN, AND P. S. BROWN.
1957. Visual pigments and depths of habitat of marine fishes. Nature (Lond.) 180:969-971.

WARRINER, J. E., J. P. MILLER, AND J. DAVIS.
1969. Distribution of juvenile river herring in the Potomac River. Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm. 23:384-388.

WHITELEY, G. C., JR.
1948. The distribution of larger planktonic Crustacea on Georges Bank. Ecol. Monogr. 18:233-264.

ZAR, J. H.
1974. Biostatistical analysis. Prentice-Hall Inc., Englewood Cliffs, N.J., 620 p.

ZINKEVICH, V. N.
1967. Observations on the distribution of herring, *Clupea harengus* L., on Georges Bank and in adjacent waters in 1962-65. Int. Comm. Northwest Atl. Fish., Res. Bull. 4:101-115.

THE COMPLETE LARVAL DEVELOPMENT IN THE LABORATORY OF *MICROPANOPE SCULPTIPES* (CRUSTACEA, DECAPODA, XANTHIDAE) WITH A COMPARISON OF LARVAL CHARACTERS IN WESTERN ATLANTIC XANTHID GENERA[1]

BRYAN L. ANDRYSZAK[2] AND ROBERT H. GORE[3]

ABSTRACT

The larval development in the laboratory of *Micropanope sculptipes*, a western Atlantic deepwater xanthid crab which inhabits encrusted and coralline substrates, is completely described and illustrated. Development proceeds from a prezoeal stage of brief duration through four zoeal stages and one megalopa stage. Survival of larvae was poor under experimental conditions of diel illumination, 36‰ salinity, and temperatures of 20°, 25°, and 25°-30° C. Development to megalopa occurred only at 25° C. Morphological characteristics of *M. sculptipes* zoeae and megalopa are compared with larval characteristics of several other western Atlantic xanthid species.

Crabs of the family Xanthidae are both numerous and diverse with species inhabiting a great variety of marine and estuarine environments (Rathbun 1930). The genus *Micropanope* was erected by Stimpson in 1871 with the type-species *Micropanope sculptipes*. This genus consists of small (12 mm carapace width) xanthid crabs with a known range from the Bahamas and Florida Keys to Brazil and Bermuda in deeper offshore oceanic water (Rathbun 1930; Guinot 1967). *Micropanope* was originally noted to resemble *Pilumnus*, and to be allied with *Panopeus*, but was supposedly distinct in being a sublittoral to bathyal group and not littoral as was *Panopeus*. However, subsequent collections yielded *Micropanope* species which were more littoral in distribution and, through time, the genus was considered to be a heterogeneous mixture of several distinct generic groups which were yet to be defined (Guinot 1967). This author emended the genus *Micropanope* to contain only two western Atlantic species: viz. *M. sculptipes* Stimpson, the type-species, and *M. lobifrons* A. Milne Edwards. The remaining species within *Micropanope* sensu lato have either been placed by Guinot in several other genera, or await placement in genera yet to be named.

Larvae of many species of xanthid crabs from several different genera have been described based on laboratory rearing, but there have been no published descriptions of a complete larval development for any species of *Micropanope* sensu lato thus far. A study on the larval development of *M. barbadensis* Rathbun has recently been completed (Gore et al. 1981), but this species will ultimately be assigned to a separate, and as yet undefined, genus close to *Coralliope* (fide Guinot 1967). A knowledge of the larval morphology of *Micropanope*, when compared with larval characteristics of previously described xanthid species, especially those species once placed in the genus *Micropanope*, may be of some utility in recognizing the evolutionary relationships among such species within the Xanthidae. Accordingly, in this report we describe the complete larval development of *M. sculptipes* from hatching to megalopa stage based on specimens raised in the laboratory, and compare these larval and postlarval stages with those from other xanthid crabs in the western North Atlantic.

MATERIALS AND METHODS

A small (9.3 mm carapace width) ovigerous female *M. sculptipes* was collected 14 June 1978 by the crew of the Harbor Branch Foundation RV *Sea Diver* (cruise SD23, station #007), with a 20 ft (6.1 m) otter trawl. The trawl sample was taken off the

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[2]Smithsonian Institution, Fort Pierce Bureau, Fort Pierce, Fla.; present address: TerEco Corporation, 500 University West, P.O. Drawer GF, College Station, TX 77840.

[3]Smithsonian Institution, Fort Pierce Bureau, Fort Pierce, FL 33450.

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coast of central eastern Florida between lat. 27°14.8′ N, long. 79°56.7′ W and lat. 27°15.1′ N, long. 79°58.0′ W from depths of 115.2-96.9 m. The specimen, collected from a substrate consisting of encrusted shell hash and *Oculina* coral, carried approximately 80 pale fuchsia eggs which darkened slightly before hatching on 20 June in the laboratory. After yielding larvae, this specimen was compared with specimens of *M. sculptipes* deposited in the National Museum of Natural History, Washington, D.C., which had been illustrated by Rathbun (1930: USNM 20719, 60777) and was found to agree in all important respects.

Three groups of 24 larvae were isolated, one each in 24 compartmented plastic boxes, and placed into controlled temperature units (CTU) at 20°, 25°, or 25°-30° C (±0.5° C) under diel illumination. Surf zone seawater (of 36‰) was filtered through glass wool fiber, stored in large Nalgene[4] bottles in the laboratory, and used to culture larvae.

Larvae received fresh seawater and were fed freshly hatched San Francisco brand *Artemia* nauplii daily. Molts and deaths of each larva and color notes of representative larval stages under refracted and reflected white light were recorded. Dead individuals and molts were preserved in 70% ethanol and were measured with a microscope fitted with an eyepiece micrometer. Measurements given are the arithmetic mean values of the number of specimens examined in each stage. Larvae were cleared in 50% lactic acid solution to which lignin pink stain was added to aid in drawing larval characters. Whole mounts (50×) and dissected appendages (drawn at 200× and checked for details at 400×) were mounted in CMCP mounting medium and drawn with Wild M5 and M20 microscopes equipped with camera lucidas.

The spent female and a complete series of larval stages are deposited in the United States National Museum, USNM 171393.

RESULTS OF REARING EXPERIMENT

Micropanope sculptipes larvae hatched as prezoeae of short, but not precisely determined, duration. They developed through four zoeal stages, after which metamorphosis to a megalopa occurred.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Figure 1 and Table 1 indicate that survival was poor and was apparently influenced by temperature. Most successful development occurred at 25° C; survival was notably lower at 20° C, and no larvae developed beyond first zoeae at 25°-30° C. Even at the "optimum" temperature of 25° C, 50% mortality occurred during the first zoeal stage and only one individual survived to the megalopa stage. At this temperature developmental duration was 26 d from hatching to megalopa; no crab stage was attained.

The duration of larval stages was variable. First stage zoeae generally required 6 or 7 d to successfully molt to second stage zoeae; however, one individual at 20° C required 15 d and another individual at 25° C persisted for 10 d before molting. These two zoeae did not survive beyond the second zoeal stage. Second and third zoeal stages generally remained as such 5 d before molting, although 20° C larvae took slightly longer than 25° C larvae. Fourth zoeal stages survived between 6 and 8 d before either molting or dying. The one fourth stage zoea at 25° C remained in stage 6 d before molting to megalopa.

Larval development was apparently regular and no larvae were observed to either skip a developmental stage or molt without developing into a more advanced stage. One zoea in the first stage at 25° C was grossly deformed when it molted to second stage at age 6 d and it died 7 d later without molting again. All other zoeae possessed similar morphological characters, so that temperature difference produced no variations. Many zoeae died during preecdysis or in ecdysis to the next larval stage. Five of the nine fourth stage zoeae died while attempting the molt to megalopae. Megalopal telsons, antennae, and chelipeds were observed beneath the transparent fourth zoeal exoskeletons of these specimens, indicating a terminal larval stage. No fifth zoeal stage larvae were observed.

The results of this study indicate that *M. sculptipes* larvae progress through four larval stages and thus are similar to the majority of xanthid species. Four zoeal stages have been considered characteristic in Xanthidae (Hyman 1925; Lebour 1928) and include many species, e.g., *Panopeus herbstii* (Costlow and Bookhout 1961a), *Eurypanopeus depressus* (Costlow and Bookhout 1961b), *Rhithropanopeus harrisii* (Chamberlain 1962), *Hexapanopeus angustifrons* (Costlow and Bookhout 1966), *Leptodius* [= *Pseudomedaeus*] *agassizii* (Costlow and Bookhout 1968), *Neopanope*

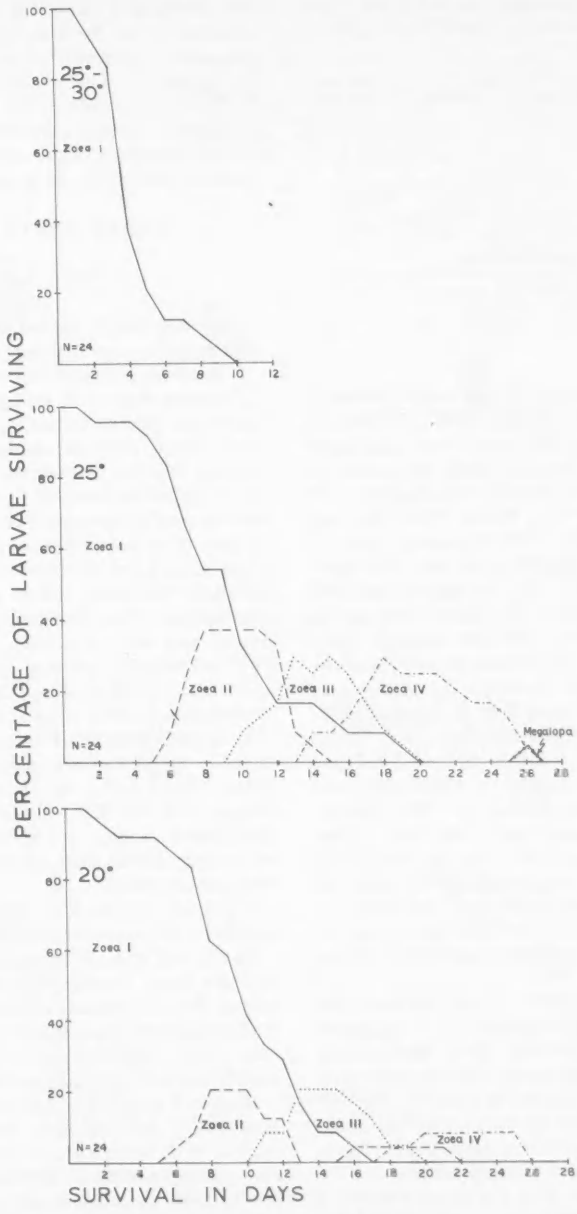

FIGURE 1.—*Micropanope sculptipes*. Percentage and duration of survival of larvae reared at three laboratory temperatures. N = number of larvae reared at each temperature in the series.

TABLE 1.—*Micropanope sculptipes*, relative duration of larval life in days at three temperatures. (Number of larvae started at each temperature = 24.)

Temp °C	Larval stage	Duration				Total no. molting to next stage
		Minimum	Mean	Mode	Maximum	
20	Zoea I	5	8	7	15	6
	Zoea II	4	—	5	5	5
	Zoea III	5	6	—	7	2
	Zoea IV	[1]6	—	—	[1]8	0
25	Zoea I	5	7	6	10	12
	Zoea II	4	—	5	5	9
	Zoea III	4	—	5	5	9
	Zoea IV	[1]1	5	6	[1]8	1
25-30	Did not survive beyond first zoeal stage					

[1]Died in stage without further molt.

texana (McMahan 1967), *N. sayi* and *N. packardii* (Costlow and Bookhout 1967), *Pilumnus dasypodus* (Sandifer 1974), and *P. sayi* (McDonald and Lang 1976). However, crabs of the genus *Menippe* develop through 5 or 6 zoeal stages prior to metamorphosis (e.g., Porter 1960; Ong and Costlow 1970; Scotto 1979), *Heterozius rotundifrons* and *Epixanthus dentatus* have two zoeal stages, and *Pilumnus lumpinus* has only one zoeal stage (Saba et al. 1978). The latter three species live in specialized and restricted habitats which may account for the differences in number of developmental stages. However, *Ozius truncatus* (four zoeal stages) and *Heteropanope (Pilumnopeus) serratifrons* (probably four zoeal stages) are also species which live in restricted habitats (Wear 1968), so other factors besides environment may influence developmental time. *Micropanope barbadensis* develops through either three or four zoeal stages (Gore et al. 1981), and the elimination of the "terminal" stage may be an adaptive response to food supply, nutritional deficiencies, or an inherited response from adult genotypes, according to several hypotheses considered by these authors.

It is therefore difficult to directly compare the duration of larval development for *M. sculptipes* (about 26 d at 25° C) with larval development times for other xanthid species. Species of *Menippe* (5 or 6 zoeal stages) required at least 17-21 d at 25° C to develop into megalopa (summarized by Scotto 1979). The duration of larval development seems to be largely dependent on temperature, and the experimental temperature conditions employed by different researchers may vary considerably for a number of reasons. Larval development time decreased for *Micropanope sculptipes* as temperature increased. This inverse relationship between temperature and duration of larval development is consistently observed for the larvae of different xanthid species (Costlow et al. 1962; Costlow and Bookhout 1971; Scotto 1979). Based on these data and at 25° C, we may postulate a planktonic development time on the order of 1 mo before metamorphosis to first crab in *M. sculptipes*.

LARVAL DESCRIPTION

First Zoea

Carapace length (anterior margin of orbit to median posterodorsal edge of carapace): 0.47 mm.

Number of specimens examined: 14.

Carapace (Figure 2A, B). Typically brachyuran, possessing rostral, dorsal, and 2 lateral spines. Eyes sessile. Rostrum straight, naked, sharply pointed, slightly shorter than carapace length. Dorsal spine about equal in length to carapace, curving gently posteriad, bearing a few scattered minute tubercles. Lateral spines short, naked, projecting perpendicular to sagittal plane. Carapace elliptical, naked except for 2 small dorsolateral setae originating midway between dorsal and lateral spines; mediodorsal knob [= "forehead protuberance" Yang 1967] naked.

Antennule (Figure 2C). Flabellate rod with 3 aesthetascs, 2 naked setae at tip.

Antenna (Figure 2D). Protopodite long, tapering to point; spirally arranged spines present along distal three-fourths length with spines larger, longer toward tip. Exopodite one-sixth to one-fifth protopodite length, naked throughout length, with 1 short apical spine, 1 long and 2 short apical nonplumose setae.

Mandibles (Figure 2E). Well-developed incisor and molar processes; no palp.

Maxillule (Figure 2F). Coxal endite with 7 stout, plumose setae. Basal endite with 5 denticulate spines, about 20 minute hairs on lateral surface. Endopodite two-segmented; proximal segment with 1 long, nonplumose seta; distal segment with 2 subterminal, 4 terminal, sparsely plumose setae.

Maxilla (Figure 2G). Coxal endite bilobed with 4 proximal, 3 distal plumose setae. Basal endite bilobed with 4 (occasionally 5) proximal and 4 distal plumose setae. Endopodite bilobed; 3 terminal sparsely plumose apical setae on proximal lobe, 5 terminal (appearing as 3 apical, 2 slightly lower) sparsely plumose setae on distal lobe; this setal formula holds for remainder of stages.

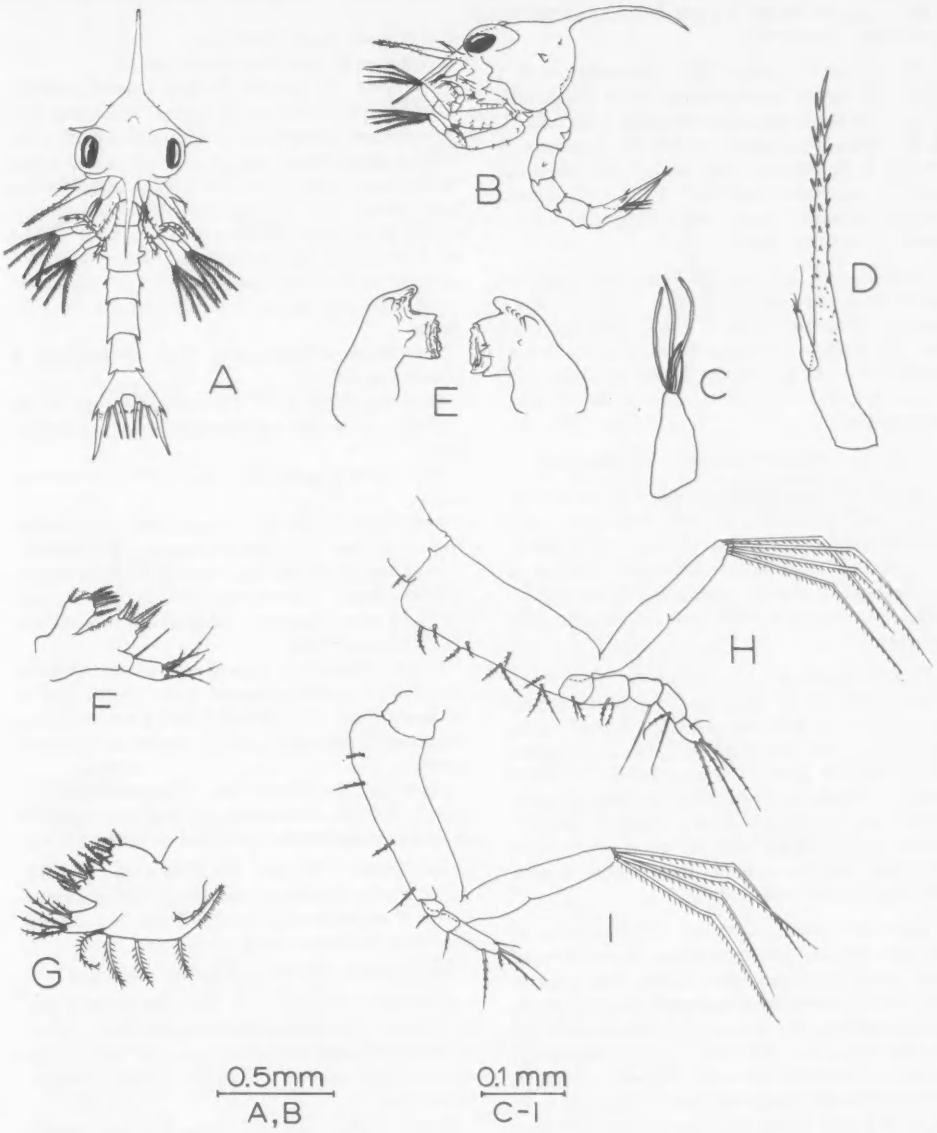

FIGURE 2.—*Micropanope sculptipes*, first zoea. A, ventral view; B, lateral view; C, antennule; D, antenna; E, mandibles; F, maxillule; G, maxilla; H, maxilliped 1; I, maxilliped 2.

Scaphognathite with 4 marginal plumose setae and elongate sharp process bearing numerous minute hairs laterally.

Maxilliped 1 (Figure 2H). Coxopodite with 1 seta. Basipodite ventral margin with 10 sparsely plumose setae arranged (proximally to distally) 2, 2, 3, 3; this setal formula holds for remainder of stages. Endopodite five-segmented with proximal to distal segment setation of 2, 2, 1, 2, 4+I. (Roman numeral denotes dorsal seta.) Exopodite with 4 terminal natatory setae.

Maxilliped 2 (Figure 2I). Coxopodite without setae. Basipodite ventral margin with one row of 4 sparsely plumose setae; this setal formula holds for remainder of stages. Endopodite three-segmented with proximal to distal segment setation of 1, 1, 4+I. Exopodite with 4 terminal natatory setae.

Maxilliped 3 and Pereiopods. Not apparent.

Abdomen (Figure 2A, B). With five somites. Somite 1 unornamented; somite 2 with anteriorly curved lateral hooks; somite 3 with smaller posteriorly curved lateral hooks. Somites 3-5 with small posterolateral spines overlapping following somite. Somites 2-5 with pair of minute posterodorsal setae.

Telson (Figure 2A, B). Bifurcate; each furca smooth, possessing one larger lateral spine near its midlength and one smaller dorsal spine originating near apex of lateral spine. Inner telson margin with 3 pairs of articulated spines, each armed throughout length with minute spinules, center pair of spines with 2 longer interior spinules and 1 longer exterior spinule located at proximal one-third of spine. Inner telson margin with pronounced medial sinus.

Color. Zoea mainly colorless with exception of localized pigment concentrations. Dorsal area of orbit pale mint green, color fading into interorbital area; interorbital protuberance faint orange. Gastric region pale orange extending along gut through first two abdominal segments (this color not due to ingested *Artemia*); diffused pale mint green surrounds orange of gastric region. Mandible incisor and molar surfaces scarlet, blending into pale orange within mandible. First and second maxillipeds with diffuse pale orange at junction of basipodite and exopodite. Proximal region of telson furcae on either side of median telson sinus tinted with diffused pale orange.

Second Zoea

Carapace length: 0.61 mm.

Number of specimens examined: 10.

Carapace (Figure 3A, B). Eyes faceted, stalked. Rostrum base with small, lateral preorbital protuberances perpendicular to longitudinal axis. Dorsal spine usually with 2 small proximal setae, occasionally with a few small widely spaced setae and tubercles. Lateral spines with 2 to 4 minute dorsal tubercles. Carapace ventral margin with 3 or 4 fringing setae; mediodorsal knob now with 4 integumental sensillae arranged into rectangle on crest, one pair setae anterior and posterior to knob.

Antennule (Figure 3C). Four aesthetascs, 2 naked setae at tip.

Antenna (Figure 3D). Unchanged except for incipient endopodite primordium near exopodite base.

Mandibles (Figure 3E). As illustrated, without palp.

Maxillule (Figure 3F). Coxal endite unchanged from first zoea. Basal endite apex with 6 denticulate spines, 1 naked seta; lateral surface with 1 plumose seta, ≈20 minute hairs. Endopodite unchanged from first zoea. Protopodite now with 1 distal plumose seta.

Maxilla (Figure 3G). Coxal endite bilobed with 4 proximal, 4 distal plumose setae. Basal endite bilobed with 5 proximal, 4 distal plumose setae. Scaphognathite with 11 or 12 marginal plumose setae.

Maxilliped 1 (Figure 3H). Coxopodite with 1 (rarely 2) seta. Endopodite unchanged from first zoea. Exopodite with 6 terminal natatory setae.

Maxilliped 2 (Figure 3I). Coxopodite without setae. Endopodite three-segmented with proximal to distal segment setation of 1, 1, 4 or 5+I. Exopodite with 7 terminal natatory setae.

Maxilliped 3 and Pereiopods. Not apparent.

Abdomen (Figure 3A, B). With five somites. Somite 1 with 1 posterodorsal seta; somites 2-5 generally unchanged from first zoea, but posterolateral spines of somites 3-5 slightly longer relative to body size.

Telson (Figure 3A, B). Generally unchanged from first zoea. An additional minute lateral furcal spine may occasionally be present within the fork created by the major lateral spine where it originates from the furca. This spine (when present) may be readily apparent, reduced to a lump,

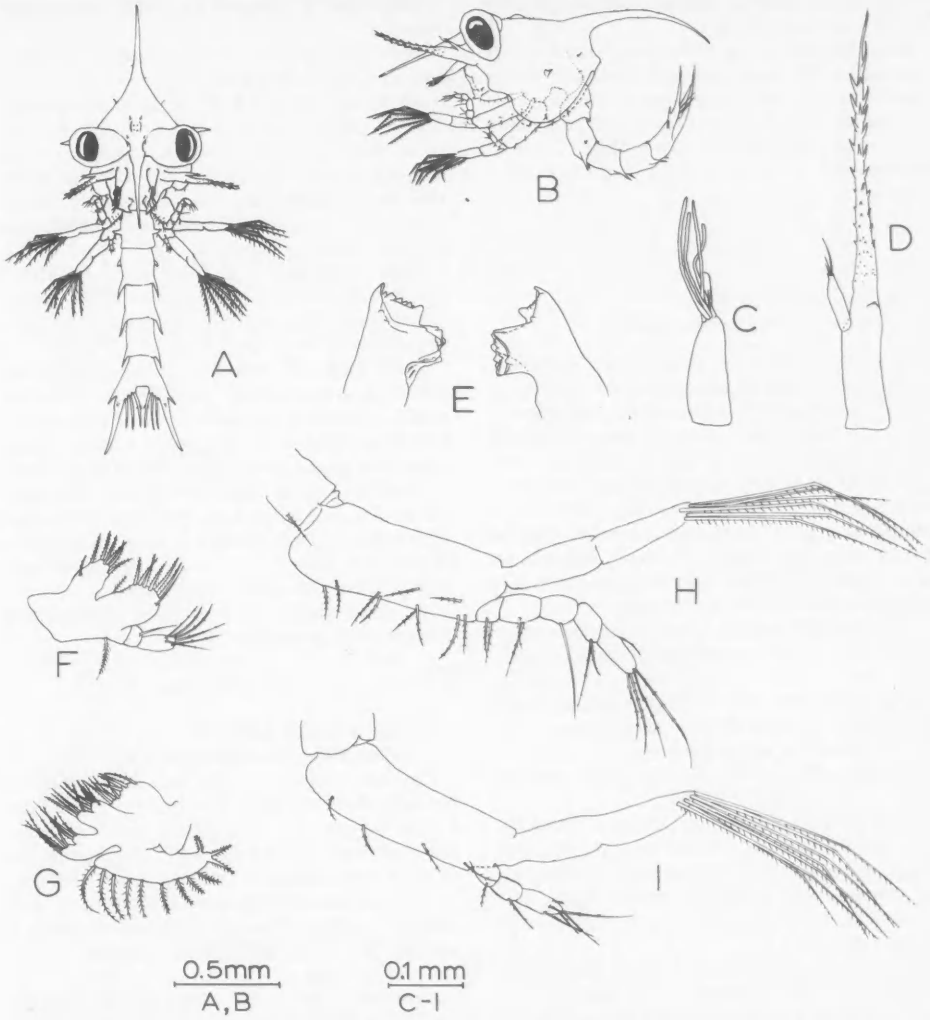

FIGURE 3.—*Micropanope sculptipes*, second zoea. A, ventral view; B, lateral view; C, antennule; D, antenna; E, mandibles; F, maxillule; G, maxilla; H, maxilliped 1; I, maxilliped 2.

or present on one furca while absent from the other on the same individual.

Color. Similar to that of first zoea, but noticeably intensified. Pale orange highlights distal three-fourths of rostrum, dorsal spine, antennae, and antennules. Gut color more burnt orange, extending through abdominal somite 4. Mandibles most pronounced in burnt orange, outer surfaces scarlet.

Third Zoea

Carapace length: 0.76 mm.
Number of specimens examined: 8.

Carapace (Figure 4A, B). Rostrum preorbital protuberances pronounced, angular. Dorsal spine with 3 (occasionally 2 or 4) small, scattered proximal setae with some scattered distal setae and minute tubercles. Lateral spines with 3 or 4 minute dorsal tubercles. Carapace ventral margin with 2 or 3 setae. Mediodorsal knob with 2 or 3 additional smaller integumental sensillae located within rectangular region previously demarcated by 4 sensillae of second zoea; 6 setae anterior, 4 setae posterior to mediodorsal knob.

Antennule (Figure 4C). With 3 aesthetascs and 1 naked seta at tip, 1 subterminal budlike projection.

Antenna (Figure 4D). Similar to earlier stage, endopodite more developed, with pointed tip slightly exceeding exopodite length.

Mandibles (Figure 4E). As illustrated, without palp.

Maxillule (Figure 4F). Coxal endite with 8 thick, plumose setae. Basal endite with 5 pectinate spines, 3 long sparsely plumose setae, 1 subterminal plumose seta, almost no minute hairs. Endopodite as in first zoea. Protopodite with 1 distal plumose seta.

Maxilla (Figure 4G). Coxal endite bilobed with 5 proximal, 4 distal plumose setae. Basal endite bilobed with 5 proximal, 4 distal plumose setae. Endopodite as in first zoea except all setae naked. Scaphognathite with 17 to 20 marginal plumose setae.

Maxilliped 1 (Figure 4H). Coxopodite with 1 (rarely 2) seta. Five-segmented endopodite setation now 2, 2, 1, 2, 5+I. Exopodite with 8 terminal natatory setae.

Maxilliped 2 (Figure 4I). Coxopodite without setae. Three-segmented endopodite setation now 1, 1, 6. Exopodite with 9 terminal natatory setae.

Maxilliped 3. Present as small, unbranched lobe.

Pereiopods (Figure 4B). Apparent as small rudiments beneath carapace.

Abdomen (Figure 4A, B). Sixth somite present, lacking posterolateral spines and posterodorsal setae. Somite 1 with 2 or 3 posterodorsal setae; somites 2-5 as in second zoea, but with posterolateral spines of somites 3-5 progressively longer; somites 2-6 developing small pleopod buds; those of somite 6 barely apparent.

Telson (Figure 4A, B). Median sinus with 2 small plumose setae. Secondary minute lateral furcal spines may or may not be present as in second zoea.

Color. Rostrum, dorsal spine, antennules, antennae nearly colorless. Maxillipeds with pale orange spreading through much of basipodites. Mandibles slightly darker burnt orange. Orbits pale mint green blending into faint sky blue at interorbital region. Sky-blue stellate chromatophore at dorsal spine base. Vandyke-brown stellate chromatophore fringed in olive, mint green, sky blue at lateral spine bases. Pereiopod buds light orange. Gut burnt orange through somite 3, with small spots of pale orange highlighting pleopod buds on somites 3-5.

Fourth Zoea

Carapace length: 0.84 mm.
Number of specimens examined: 9.

Carapace (Figure 5A, B). Rostrum preorbital protuberances recurved into anteriorly directed hooks. Dorsal spine with 4 small proximal setae, few scattered minute tubercles. Lateral spines as in third zoea. Carapace ventral margin with 6-11 (usually 9) setae. Mediodorsal knob with 4 outer sensillae (arranged as rectangle) surrounding 4 smaller inner sensillae; 10 setae anterior, 4 setae posterior to knob.

Antennule (Figure 5C). Biramous. Endopodite half exopodite length, naked, pointed at tip. Exopodite two-segmented with 12 aesthetascs arranged proximally to distally (2, 6) (1, 3 apical) plus 1 naked seta at tip. Protopodite swollen proximoventrally, supporting 2 minute plumose setae.

Antenna (Figure 5D). Endopodite at least one-half protopodite length.

Mandibles (Figure 5E). As illustrated; palp present.

Maxillule (Figure 5F). Coxal endite with 11 or 12 setae (small proximal seta occasionally absent).

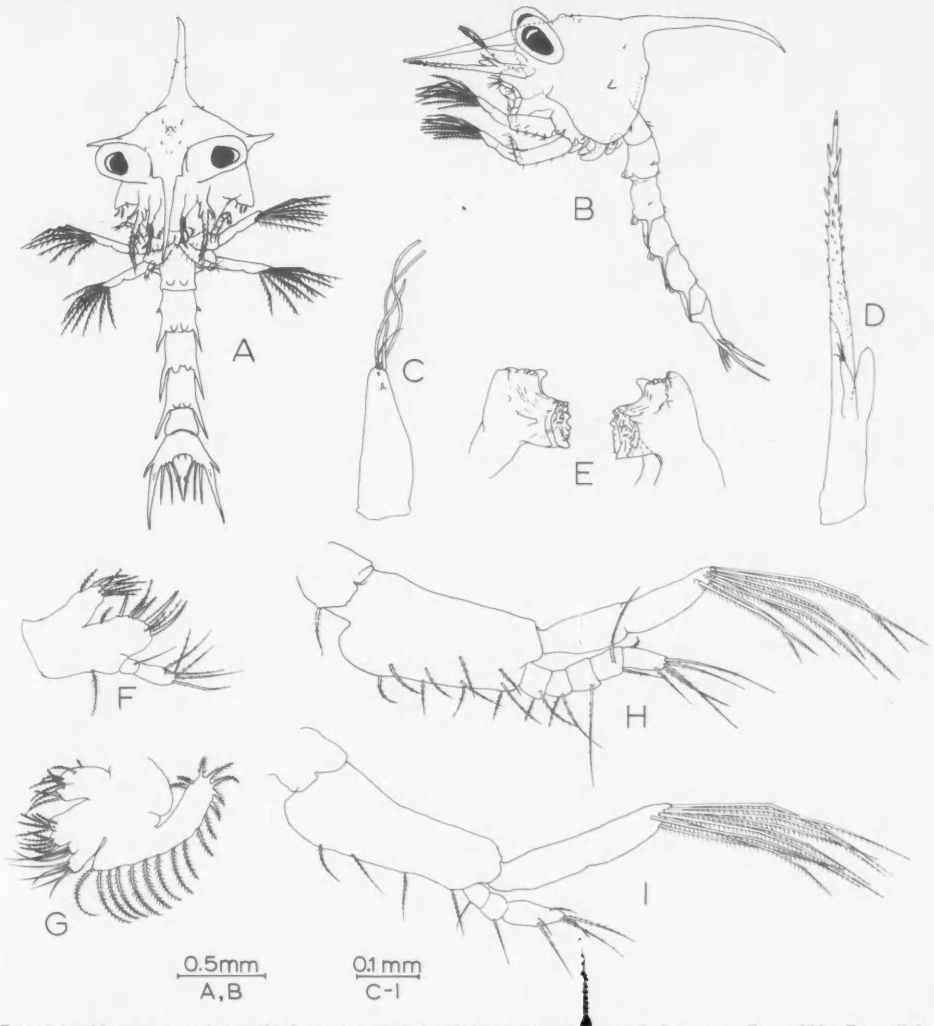

FIGURE 4.—*Micropanope sculptipes*, third zoea. A, ventral view; B, lateral view; C, antennule; D, antenna; E, mandibles; F, maxillule; G, maxilla; H, maxilliped 1; I, maxilliped 2.

FIGURE 5.—*Micropanope sculptipes*, fourth zoea. A, ventral view; B, lateral view; C, antennule; D, antenna; E, mandibles; F, maxillule; G, maxilla; H, maxilliped 1; I, maxilliped 2; J, maxilliped 3.

Basal endite with 7 denticulate spines, 5 or 6 sparsely plumose setae; few minute hairs. Endopodite and protopodites as in third zoea.

Maxilla (Figure 5G). Coxal endite bilobed with 6 proximal, 4 distal plumose setae. Basal endite bilobed with 6 proximal, 7 distal plumose setae, several minute lateral hairs on distal lobe. Scaphognathite with 25 to 30 (usually 28 or 29) marginal plumose setae.

Maxilliped 1 (Figure 5H). Coxopodite with 2 (rarely 1) setae. Endopodite as in third zoea. Exopodite with 9 terminal natatory setae.

Maxilliped 2 (Figure 5I). Coxopodite with no (rarely 1 very small) seta. Three-segmented endopodite setation 1, 1, 5+I (rarely 4+I). Exopodite with 11 terminal natatory setae.

Maxilliped 3 (Figure 5J). Greatly enlarged from third zoea, epipodite and endites well developed, not yet segmented.

Pereiopods (Figure 5A, B). Greatly enlarged from third zoea, with incipient segmentation and differentiation.

Abdomen (Figure 5A, B). Somite 1 with 3 posterodorsal setae, slight posterolateral projections. Somites 2-6 as in third zoea but pleopod buds enlarged and biramous on somites 2-5, small and uniramous on somite 6.

Telson (Figure 5A, B). Median sinus with 3 or 4 small plumose setae. Secondary minute lateral furcal spines may or may not be present as in second zoea.

Color. Rostrum, antennules, antennae pale orange. Maxilliped 1 and 2 basipodites proximally with prominent burnt-orange stellate chromatophores, diffused with pale mint green at basipodite-exopodite junction. Mandible incisor and molar surfaces fringed in dark Vandyke brown blending into scarlet and burnt orange. Orbits pale mint green. Sky-blue stellate chromatophore mixed with pale green and yellow at dorsal spine base. Lateral spines with burnt-orange and Vandyke-brown stellate chromatophores blending into mint green distally. Body (cephalothorax) generally pale yellow-orange mixed with faint mint green. Gastric region and gut burnt orange extending through abdominal somite 3. Abdominal somites 2-5 with paired patches of pale burnt orange lateral to pleopod bud origins, otherwise colorless. Telson entirely pale orange diffused with mint green in vicinity of lateral and dorsal furcal spines.

Megalopa

Carapace length (rostrum tip to median posterior margin) × greatest width: 1.25 mm × 1.20 mm.

Number of specimens examined: 1.

Carapace (Figure 6A-C). Slightly longer than wide, subrectangular, somewhat inflated. Frontal region produced, highly sculptured; rostrum prominent, acutely triangular, sharply rounded, becoming broader at base, recurving anteriad into prominent anterolateral horns; latter one-half rostrum length, each with a small lateral spine bearing 2 small apical setae near base, oriented perpendicular to longitudinal axis of horn. Four prominent plumose setae equal in length to rostrum project anteriorly between rostrum base and base of each horn. Several smaller setae scattered in interorbital, gastric, and cardiac regions. One small tubercle projecting near median posterodorsal margin. Numerous setae fringe posterior and ventrolateral margins.

Antennule (Figure 6D). Biramous; peduncle three-segmented; proximal article with 2 small plumose setae and 1 naked seta, penultimate article with 1 naked seta, ultimate article with 2 small lateral setae and 6 nearly terminal, long, naked setae (arranged as 3 on either side of segmented flagellum). Ventral ramus with 3 terminal, 1 slightly subterminal, naked setae; dorsal ramus with aesthetascs progressing distally as follows: (8), (6, +1 plumose seta opposite), (3 lateral, +3 nonplumose setae near tip).

Antenna (Figure 6E). Peduncle with 3 lateral setae, a distal lobe; setation (proximally to distally) on flagellar articles 1, 1, 0, 3, 4, 0, 0, 5. Articles 5 and 6 slightly constricted at midlength, may be partially segmented.

Mandibles, maxillule, maxilla, and *maxillipeds 1* and *2*. These were not dissected from the specimen to prevent the destruction of the only megalopa obtained.

Maxilliped 3 (Figure 6F). Coxopodite and epipodite not exposed for examination. Basipodite partially exposed with at least 16 short setae. Endopodite five-segmented, setation progressing distally 16, 14, 8, 12, 8 (5 lateral, 3 apical). Exopodite two-segmented; proximal segment with 3 lateral setae, distal segment with 1 subterminal seta and 6 long, plumose terminal setae.

Pereiopods (Figure 6A-C, 6G-I). All bear numerous setae. Chelipeds (Figure 6G) similar, equal;

FIGURE 6.—*Micropanope sculptipes*, megalopa. A, dorsal view; B, lateral view; C, ventral view; D, antennule; E, antenna; F, maxilliped 3; G, cheliped; H, pereiopod 3; I, pereiopod 5; J, pleopod from abdominal somite 3; K, abdominal somite 6 with pleopods, telson.

coxa with small basal tubercle, ischium with large hooked spine and small dorsal tubercle. Bases of pereiopods 2-5 (Figure 6H, I) with small median spine; dactyls of pereiopods 2-4 with a row of 3 subterminal serrated spines, 1 terminal spine; dactylus of pereiopod 5 with 1 subterminal serrated spine, 3 long subterminal setae, 1 terminal spine.

Abdomen (Figure 6A-C). With 6 somites and telson. Lateral pleura of somites 2-5 slightly overlap following segment; lateral hooks of somites 2 and 3 absent. Numerous setae cover dorsal surfaces and posterodorsal margins of all somites. Pleopods biramous (Figure 6J) on somites 2-5, uniramous on somite 6 (Figure 6K); exopodites with plumose setae arranged (anteriorly to posteriorly) 15 or 16, 13 or 14, 13 or 14, 11, 7 or 8; endopodites of pleopods 2-5 with appendix interna consisting of 2 terminal curved hooks.

Telson (Figure 6K). Roughly rectangular with 2 pairs of dorsal setae. Lateral margins produced posteriorly, forming slightly extended lobes, each lobe bearing 3 serrated spines of variable length; posterior margin shallowly sinuous, with 3 plumose setae.

Color. The one megalopa died before color notes could be made.

DISCUSSION

Comparative Morphology of *Micropanope sculptipes* With Other Xanthid Larvae

The Xanthidae is a large and heterogeneous family containing many genera and numerous species. As a consequence, the larval stages of many such species from the Atlantic and Pacific Oceans have been studied over a long period (e.g., Lebour 1928; Aikawa 1929, 1937; Wear 1968; Saba et al. 1978). In the western Atlantic, larval development is reliably known either completely or in part for at least 10 genera and 15 species, in addition to several other genera and species which are less certain because identifications were based on planktonic material. As might be expected, there exist numerous characters, both shared and unshared, in the larval stages, so that comparison among the species and genera is often quite difficult. Readily observable morphological characters useful in distinguishing zoeae and megalopae of *M. sculptipes* from other western Atlantic xanthid species which may cooccur in the plankton include those of the rostral spine, antenna, anterodorsal carapace setae, abdominal spination, telsonal furcae spination, and armature on basal segments of the pereiopods.

Within the genus *Micropanope* (sensu lato), *M. sculptipes* exhibits extremely close morphological similarity (but not developmental similarity) with the larvae of *M. barbadensis* (Gore et al. 1981). Both species exhibit a type of antenna different from the four categories established by Aikawa (1929) necessitating the creation of a fifth category, Type E (Gore et al. 1981). This grouping contains those larvae (presently only the two species here considered) in which the antennal exopodite is from one-fourth to one-seventh total protopodite length. Other features allowing distinction between the two species include (in *M. sculptipes*) the unadorned rostral carapace spine, shorter lateral spines, unpaired lateral spines on the telsonal furcae, a less lunate telson, more distinct spination on the antennal protopodite, a single coxal seta on maxilliped 1, and the general distribution of fine hairs on the anterodorsal area of the carapace. The position and number of integumentary sensillae may prove to be of some value, but this feature in the genus has only been described for *M. sculptipes*. Gore et al. (1981) worked with molted carapaces in describing *M. barbadensis* and were unable to distinguish these sensory pits clearly.

A comparison of the larvae of *M. sculptipes* with those in other western Atlantic xanthid species is summarized in Table 2. The following differences appear salient. The preorbital rostral hooks of *M. sculptipes*, which are fully formed in the fourth zoeal stage, are similar to, yet larger than, those described for *Panopeus herbstii*. *Pseudomedaeus* [ex *Leptodius*] *agassizii* also possesses similar "secondary rostral spines," but these are much more prominent from its second through fourth zoeal stages. The rostrum of the other species noted (see Table 2) remains generally straight and unarmed throughout development.

The antenna of *M. sculptipes* consists of a spinous protopodite and has an exopodite which is one-sixth the protopodite length. The species in other genera possess an antennal protopodite which is either nonspinous or noticeably less spinous than that of *Micropanope*. The antennal exopodite of these xanthid zoeae fall into three general categories as described by Lebour (1928): equal to protopodite length or Type A (*Pilumnus sayi, P. dasypodus*); one-half to three-fourths protopodite length or Type B (*Menippe mercenaria, M.*

TABLE 2.—Comparison of morphologically important zoeal characters for distinguishing *Micropanope sculptipes* larvae from other western Atlantic species of Xanthidae based on descriptions and illustrations from different sources (only the first four zoeal stages of *Menippe mercenaria* and *M. nodifrons* are considered).

Species (source of description)	Rostrum	Antenna	Anterodorsal carapace setae	Abdomen spination	Telson furca spination
		First zoea			
Micropanope sculptipes	Straight, unarmed, ≈carapace length	Protopodite: spinous distal 3/4 Exopodite: 1/6-1/5 protopodite length, 3 apical setae	None	Posterolateral spines somites 3-5 equal, smooth Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine, 1 lateral spine
Neopanope sayi (Chamberlain 1961)	Straight, unarmed, 2× carapace length	Protopodite: unarmed Exopodite minute, apical seta	None figured	Posterolateral spines somites 3-5 equal, smooth Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine
Neopanope texana (McMahan 1967)	Straight, unarmed, ≈carapace length	Protopodite: unarmed Exopodite minute, apical seta	None	Posterolateral spines somites 3-5 equal, smooth Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine
Neopanope packardii (Costlow and Bookhout 1967)	Straight, unarmed, ≈carapace length	Protopodite: sparsely spinous tip Exopodite: minute spine	None figured	Posterolateral spines somites 3-5 equal, smooth Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine
Panopeus herbstii (Costlow and Bookhout 1961a)	Straight, unarmed, ≈carapace length	Protopodite: spinous tip Exopodite minute, apical spine	None figured	Posterolateral spines somites 3-5 equal, smooth Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine, 2 lateral spines
Eurypanopeus depressus (Costlow and Bookhout 1961b)	Straight, unarmed, 1.5× carapace length	Protopodite: spinous distal 1/3 Exopodite minute, apical spine	None figured	Posterolateral spines somites 3-5 equal, smooth Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine
Hexapanopeus angustifrons (Costlow and Bookhout 1966)	Straight, unarmed, 1.5× carapace length	Protopodite: unarmed Exopodite minute	None figured	Lateral hooks somites 2,3	Furca smooth
Rhithropanopeus harrisii (Chamberlain 1962)	Straight, unarmed, 2.5 × carapace length	Protopodite: minute spinules distal 1/4 Exopodite minute	None figured	Posterolateral spines somites 4, 5 prominant Lateral hooks somite 2	Furca smooth: 1 dorsal spine
Pseudomedaeus agassizii (Costlow and Bookhout 1968)	Straight, unarmed, ≈carapace length	Protopodite: spinous distal 1/2 Exopodite: 1/10 protopodite length, 2 apical setae	None figured	Posterolateral spines somites 3-5 equal, smooth Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine, 2 lateral spines
Eurytium limosum (Kurata[1])	Straight, unarmed, ≈carapace length	Protopodite: spinous distal 1/3 Exopodite minute, apical seta	None figured	Posterolateral spines somites 3-5 smooth, subequal Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine, 1 lateral spine, 1 minute lateral seta
Pilumnus sayi (Kurata[1])	Unarmed, 1/3 carapace length	Protopodite: spinous distal 1/2 Exopodite = protopodite length, spinous distal 1/2, 2 mid-lateral spines	None figured	Posterodorsal margins somites 2-5 serrated Lateral hooks somites 2-5	Furca spinous: 1 dorsal spine, 2 lateral spines
Pilumnus dasypodus (Sandifer 1974)	Unarmed, 1/3 carapace length	Protopodite: spinous distal 1/2 Exopodite = protopodite length, spinous distal 1/2, 2 mid-lateral spines	None figured	Posterodorsal margins somites 3-5 serrated Lateral hooks somites 2,3	Furca spinous: 1 dorsal spine, 2 lateral spines
Menippe mercenaria (Porter 1960)	Straight, unarmed, ≈ carapace length	Protopodite: spinous distal 1/2-1/5 Exopodite: 3/4 protopodite length, apical spine 1/2-3/5 exopodite length	None figured	Dorsolateral spines somites 4, 5 Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine, 1 lateral spine
Menippe nodifrons (Scotto 1979)	Straight, unarmed, ≈carapace length	Protopodite: spinous distal 1/2-1/5 Exopodite: 3/4 protopodite length, apical spine 2/5 exopodite length	None	Dorsolateral spines somite 5 Lateral hooks somites 2,3	Furca smooth: 1 dorsal spine, 2 lateral spines

TABLE 2.—*Continued.*

Species (source of description)	Rostrum	Antenna	Anterodorsal carapace setae	Abdomen spination	Telson furca spination
		Second zoea			
Micropanope sculptipes	Small preorbital protuberances	Protopodite, exopodite unchanged[2]	4	Unchanged[2]	Furca smooth: 1 dorsal spine, 1 or 2 lateral spines
Neopanope sayi (Chamberlain 1961)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Neopanope texana (McMahan 1967)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None	Unchanged[2]	Unchanged[2]
Neopanope packardii (Costlow and Bookhout 1967)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Panopeus herbstii (Costlow and Bookhout 1961a)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Eurypanopeus depressus (Costlow and Bookhout 1961b)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Hexapanopeus angustifrons (Costlow and Bookhout 1966)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Posterolateral spines somites 3-5 equal, smooth Lateral hooks unchanged[2]	Unchanged[2]
Rhithropanopeus harrisii (Chamberlain 1962)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Pseudomedaeus agassizii (Costlow and Bookhout 1968)	Secondary rostral spines	Protopodite: spinous distal 1/3 Exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Eurytium limosum (Kurata[1])	Unchanged[2]	Protopodite smooth, Exopodite unchanged[2]	Not given	Unchanged[2]	Unchanged[2]
Pilumnus sayi (Kurata[1])	Unchanged[2]	Protopodite, exopodite unchanged[2]	Not given	Unchanged[2]	Unchanged[2]
Pilumnus dasypodus (Sandifer 1974)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Menippe mercenaria (Porter 1960)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Posteroventral spines somites 3-5; otherwise unchanged[2]	Unchanged[2]; spines minute
Menippe nodifrons (Scotto 1979)	Unchanged[2]	Protopodite: unchanged[2] Exopodite: spine slightly longer	4	Posteroventral spines somites 3, 4; posteroventral tooth somite 5; otherwise unchanged[2]	Unchanged[2]; spines minute
		Third zoea			
Micropanope sculptipes	Angular preorbital protuberances	Protopodite: spinous distal 2/3 Exopodite unchanged[2]	10	Unchanged[2]	Unchanged[3]
Neopanope sayi (Chamberlain 1961)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Neopanope texana (McMahan 1967)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None	Unchanged[2]	Unchanged[2]
Neopanope packardii (Costlow and Bookhout 1967)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Panopeus herbstii (Costlow and Bookhout 1961a)	Small preorbital protuberances	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Eurypanopeus depressus (Costlow and Bookhout 1961b)	Unchanged[2]	Protopodite: spinous tip Exopodite miniscule	None figured	Unchanged[2]	Unchanged[2]
Hexapanopeus angustifrons (Costlow and Bookhout 1966)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[3]	Unchanged[2]
Rhithropanopeus harrisii (Chamberlain 1962)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Pseudomedaeus agassizii (Costlow and Bookhout 1968)	Secondary rostral spines 1/3 rostrum length	Protopodite, exopodite unchanged[3]	None figured	Unchanged[2]	Unchanged[2]
Eurytium limosum (Kurata[1])	Unchanged[2]	Protopodite, exopodite unchanged[3]	Not given	Unchanged[2]	Unchanged[2]
Pilumnus sayi (Kurata[1])	Unchanged[2]	Protopodite, exopodite unchanged[2]	Not given	Unchanged[2]	Unchanged[2]
Pilumnus dasypodus (Sandifer 1974)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Menippe mercenaria (Porter 1960)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[3]	Unchanged[3]
Menippe nodifrons (Scotto 1979)	Unchanged[2]	Protopodite, exopodite unchanged[3]	4	Unchanged[3]	Unchanged[3]

TABLE 2.—*Continued.*

Species (source of description)	Rostrum	Antenna	Anterodorsal carapace setae	Abdomen spination	Telson furca spination
		Fourth zoea			
Micropanope sculptipes	Preorbital hooks	Protopodite: spinous distal 1/3 Exopodite unchanged[3]	14	Unchanged[2]	Unchanged[3]
Neopanope sayi (Chamberlain 1961)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Neopanope texana (McMahan 1967)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None	Unchanged[2]	Unchanged[2]
Neopanope packardii (Costlow and Bookhout 1967)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Panopeus herbstii (Costlow and Bookhout 1961a)	Small preorbital hooks	Protopodite: unchanged[2] Exopodite miniscule	None figured	Unchanged[2]	Unchanged[2]
Eurypanopeus depressus (Costlow and Bookhout 1961b)	Unchanged[2]	Protopodite, exopodite unchanged[4]	None figured	Unchanged[2]	Unchanged[2]
Hexapanopeus angustifrons (Costlow and Bookhout 1966)	Unchanged[2]	Protopodite: unchanged[2] Exopodite miniscule	None figured	Unchanged[3]	Unchanged[2]
Rhithropanopeus harrisii (Chamberlain 1962)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Pseudomedaeus agassizii (Costlow and Bookhout 1968)	Unchanged[4]	Protopodite, exopodite unchanged[3]	None figured	Unchanged[2]	Unchanged[2]
Eurytium limosum (Kurata[1])	Unchanged[2]	Protopodite, exopodite unchanged[3]	Not given	Unchanged[2]	Unchanged[2]
Pilumnus sayi (Kurata[1])	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[2]	Unchanged[2]
Pilumnus dasypodus (Sandifer 1974)	Unchanged[2]	Protopodite, exopodite unchanged[2]	1(?) figured	Unchanged[2]	Unchanged[2]
Menippe mercenaria (Porter 1960)	Unchanged[2]	Protopodite, exopodite unchanged[2]	None figured	Unchanged[3]	Unchanged[3]
Menippe nodifrons (Scotto 1979)	Unchanged[2]	Protopodite, exopodite unchanged[2]	8	Posterolateral spines somites 3, 4, dorsolateral spines somite 5 longer	Unchanged[4]

[1]Kurata, H. 1970. Studies on the life histories of decapod Crustacea of Georgia. Unpubl. rep., 274 p. Univ. Georgia Mar. Inst., Sapelo Island.
[2]Character unchanged from first zoea.
[3]Character unchanged from second zoea.
[4]Character unchanged from third zoea.

nodifrons); minute or Type C (*Neopanope sayi, N. texana, N. packardii, Panopeus herbstii, Eurypanopeus depressus, Hexapanopeus angustifrons, Rhithropanopeus harrisii, Pseudomedaeus agassizii, Eurytium limosum*). The antennal exopodite of *Micropanope sculptipes* (Type E) is thus distinctive from other xanthid larvae both in its length relative to the protopodite length, and in armature. Although the antenna of *P. agassizii* closely resembles that of *M. sculptipes*, the protopodite is less spinous and the exopodite is one-tenth the protopodite length with two apical setae.

The anterodorsal carapace (anterior half of the dorsal carapace surface) setae of *M. sculptipes* zoeae first appear in the second stage (2), and number 10 and 14 in the third and fourth stages, respectively. Anterodorsal carapace setae are not described for most of the other xanthid species; one seta is illustrated in the fourth stage of *Pilumnus dasypodus*, and *Menippe nodifrons* develops 4 setae during its second and third stages and 8 setae in its fourth stage. These setae are present in stage II zoeae of *Micropanope barbadensis* (1-2), stage III (4), and stage IV (12-14).

Micropanope sculptipes zoeae have abdominal spination characteristics which consist of lateral hooks on the second and third abdominal somites, and smooth posterolateral spines on the third through fifth abdominal somites. The posterolateral spines increase in length with each succeeding zoeal stage. This pattern of abdominal spination is similar to that observed for most other xanthid species, but some species vary. *Hexapanopeus angustifrons* does not possess posterolateral spines in the first stage, but develops them in subsequent stages in a manner similar to *M. sculptipes*. *Rhithropanopeus harrisii* possesses lateral hooks only on the second somite and conspicuously long posterolateral spines on the fourth and fifth somites. *Pilumnus sayi* has serrated posterodorsal margins and lateral hooks on the second through fifth somites, and *P. dasypodus* has serrated posterodorsal margins on the third through fifth somites and lateral hooks on the

second and third somites. *Menippe mercenaria* and *M. nodifrons* possess lateral hooks on the second and third somites. *Menippe mercenaria* has a large pair of dorsolateral spines on the fourth and fifth somites, and develops posteroventral spines on the third through fifth somites in its second and subsequent zoeal stages. *Menippe nodifrons* has a large pair of dorsolateral spines only on the fifth somite, and develops posteroventral spines only on the third and fourth somites in its second and subsequent zoeal stages.

Spination of the zoeal telson furca is varied among xanthid species. *Micropanope sculptipes* first zoeae have smooth telson furcae with 1 dorsal and 1 lateral spine. Second and subsequent zoeal stages have furcae with 1 dorsal spine, and 1 or 2 lateral spines. *Neopanope sayi, N. texana, N. packardii, Eurypanopeus depressus*, and *Rhithropanopeus harrisii* have smooth telson furcae with only 1 dorsal spine. *Panopeus herbstii* and *Pseudomedaeus agassizii* have smooth telson furcae with 1 dorsal spine and 2 lateral spines. *Hexapanopeus angustifrons* has smooth telson furcae without dorsal or lateral spines. *Pilumnus sayi* and *P. dasypodus* have spinous telson furcae with 1 dorsal spine and 2 lateral spines. The telson furcae of *Menippe* are smooth and bear minute spines; *M. mercenaria* has 1 dorsal and 1 lateral furcal spines, and *M. nodifrons* has 1 dorsal and 2 lateral furcal spines.

Micropanope sculptipes megalopae may be quickly distinguished from those of *M. barbadensis*, because the latter is presently the only species within the genus which bears spines on the coxabases and ischia; in *M. sculptipes* only the bases are so armed.

Micropanope sculptipes may be separated from other xanthid megalopae by examining the frontal region ornamentation and telson structure (Table 3). The frontal region of *M. sculptipes* is ornamented with a prominent rostrum and lateral horns; each lateral horn has a small lateral spine near its base. Four long, plumose setae lay between the rostrum and each lateral horn. *Panopeus herbstii, Neopanope packardii*, and *Pseudomedaeus agassizii* have pointed, depressed rostrums. The lateral spines (horns) of *N. packardii* are short, and the frontal region is devoid of setae. *Panopeus herbstii* and *Pseudomedaeus agassizii* have conspicuous lateral spines with 1 seta and 2 setae, respectively, between the rostrum and each lateral spine. The remaining species discussed herein have rostrums which are reduced, broad, and generally rounded. The lateral spines of *Neopanope sayi* and *N. texana* are short and there are 5 setae and 2 setae, respectively, between the rostrum and each lateral spine. *Hexapanopeus angustifrons* and *Eurytium limosum* have prominent lateral horns which equal or exceed the rostrum length. Five setae and two setae are present between the rostrum and each lateral spine in *H. angustifrons* and *E. limosum*, respectively. No lateral horns are found in *Rhithropanopeus harrisii* or *Eurypanopeus depressus*; 2 setae are found lateral to the rostrum in the former species while no setae are present in the latter species. No lateral horns are found in *Pilumnus sayi* or *P. dasypodus*, and 3 setae are present on either side of the rostrum in both species. The rostrums of *Menippe mercenaria* and *M. nodifrons* are broad and have a distinct median cleft. No lateral horns or setae are present in *M. mercenaria*, but bluntly angular interorbital protuberances and a few small, scattered setae are found in the frontal region of *M. nodifrons*.

The telson of *Micropanope sculptipes* is rectangular with 2 pairs of dorsal setae, 3 serrated spines at each posterolateral angle, and 3 plumose setae along the shallow median telson sinus. Rectangular telsons are found in *E. depressus, H. angustifrons, Pseudomedaeus agassizii*, and *R. harrisii*. *Eurypanopeus depressus* has 3 short caudal setae with 2 longer setae on either side. *Hexapanopeus angustifrons* and *P. agassizii* have 2 to 4 short setae and 4 short setae, respectively, along the posterior telson margin. *Rhithropanopeus harrisii* has a few short setae along its posterior telson margin. Rounded (convex) posterior telson margins are found in *N. sayi, M. texana, N. packardii, Panopeus herbstii*, and *Eurytium limosum*. *Neopanope texana* has 3 pairs of dorsal telson setae and 3 setae along the posterior telson margin, and *N. packardii* has 8 stiff spines along its telson caudal margin. *Panopeus herbstii* has 3 to 6 stiff caudal telson spines. The telsons of *Pilumnus sayi* and *P. dasypodus* are posteriorly rounded; *P. dasypodus* has 2 dorsal and 2 ventral setae, and a posterior border which is generally unarmed. *Menippe mercenaria* has a rounded and somewhat truncated posterior telson margin. The telson of *M. nodifrons* is subquadrate with 5 setae along its posterior margin; other telson setation is variable.

Plesiomorphy and Larval Development

Scotto (1979) provided a detailed discussion of

TABLE 3.—Comparison of morphologically important megalopal characters for distinguishing *Micropanope sculptipes* from megalopae of other western Atlantic species of Xanthidae based on descriptions and illustrations from different sources.

Species (description source)	Frontal region	Telson
Micropanope sculptipes	Rostrum prominent, sharply rounded Lateral horns prominent, 1/2 rostrum length, small lateral spines bearing 2 apical setae 4 long, plumose setae between rostrum and each lateral spine	Rectangular, 2 pairs dorsal setae, 3 serrated spines at each outer corner, 3 plumose setae along shallow median sinus
Neopanope sayi (Chamberlain 1961)	Rostrum square, depressed into blunt bifid tooth Lateral spines blunt 5 short setae between rostrum and each lateral spine	Rounded posteriorly
Neopanope texana (McMahan 1967)	Rostrum blunt, depressed, notched Lateral spines small, pointed 2 short setae between rostrum and each lateral spine	Rounded posteriorly, 3 pairs dorsal setae, 3 posterior setae
Neopanope packardii (Costlow and Bookhout 1967)	Rostrum long, pointed, depressed Lateral spines short, pointed No frontal setae figured	Caudal margin with 8 stiff spines
Panopeus herbstii (Costlow and Bookhout 1961a)	Rostrum stoutly pointed, depressed Lateral spines stout, pointed slightly less than rostrum length 1 stout seta between rostrum and each lateral spine	Rounded posteriorly, 3-6 stiff caudal spines
Eurypanopeus depressus (Costlow and Bookhout 1961b)	Rostrum blunt, broadly triangular, depressed No lateral spines or frontal setae	Rectangular, posterior margin with 3 short caudal setae, 2 longer setae on each side
Hexapanopeus angustifrons (Costlow and Bookhout 1966)	Rostrum broad, rounded, depressed Lateral horns prominent 5 short setae between rostrum and each lateral horn	Rectangular, posterior margin with 2-4 short setae
Rhithropanopeus harrisii (Chamberlain 1962)	Rostrum blunt, depressed bifid tooth No lateral spines 2 short setae on each side of rostrum	Rectangular, few short setae on posterior margin
Pseudomedaeus agassizii (Costlow and Bookhout 1968)	Rostrum pointed, depressed Lateral spines stout, pointed, slightly shorter than rostrum 2 small setae between rostrum and each lateral spine	Rectangular, 4 short setae on posterior margin
Eurytium limosum (Kurata[1])	Rostrum blunt, depressed bifid tooth Lateral horns prominent =rostrum length 3-4 setae between rostrum and each lateral horn, 1 outer lateral horn seta	Rounded posteriorly
Pilumnus sayi (Kurata[1])	Rostrum short, blunt, depressed No lateral spines 3 short setae on each side of rostrum	Rounded posteriorly
Pilumnus dasypodus (Sandifer 1974)	Rostrum broad, rounded, depressed No lateral spines or frontal setae	Rounded, 2 dorsal, 2 ventral setae; posterior border unarmed (rarely with 1, 2 small medial spines)
Menippe mercenaria (Kurata[1]) *Menippe nodifrons* (Scotto 1979)	Rostrum broad, depressed, shallow median groove No lateral spines or frontal setae figured Rostrum strongly deflexed, blunt, rounded, distinct median cleft Interorbital prominences lateral to rostrum angular, blunt	Rounded, somewhat truncated posterior margin Subquadrate, 5 setae on posterior margin, other setation variable

[1]Kurata, H. 1970. Studies on the life histories of decapod Crustacea of Georgia. Unpubl. rep., 274 p. Univ. Georgia Mar. Inst., Sapelo Island.

the importance of larval characters in determining phylogenetic relationships among brachyuran taxa, with special reference to the genus *Menippe*, and the families Xanthidae and Cancridae. Although Lebour (1928) enumerated several distinguishing morphological characters of xanthid larvae, including number of zoeal stages, carapacial armature, antennal morphology, abdominal morphology, and telson armature, Wear (1968, 1970) has shown that few of these are now valid. Even so, the larval characteristics of *Micropanope sculptipes* generally agree with Lebour's classical categorization of morphological characteristics of the Xanthidae. Moreover, the antennal structure of *M. sculptipes* differs in important respects, distinctive for the genus.

Hyman (1925) and Lebour (1928) divided the antennal morphology of xanthid larvae into two or three distinctive groups: antennal exopodite either minute, nearly equal to protopodite length, or about three-fourths protopodite length. Shorter antennal exopodites were considered indicative of evolutionarily more advanced species.

Aikawa (1929) recognized four types of antennae (A, B, C, D), also based on the relative length of the peduncle (= protopodite) to that of the exopodite. In Type A the protopodite and exopodite are nearly equal in length, a condition considered most primitive; in Type B the exopodite is one-half to three-fourths of the protopodite length, a type characteristic of most brachyuran zoeae; in Type C the exopodite is minute, these are the most highly developed. Type D antennae have a simple, inconspicuous spiny process which is shorter than either the rostrum or the antennule, and is considered to be a deviation.

The antennal exopodite of larval *M. sculptipes* is one-sixth to one-fifth the length of the protopodite, and therefore may be considered an intermediate form in the antennal classification schemes of Hyman (1925), Lebour (1928), and Aikawa (1929). The antennal configuration of *M. sculptipes* has been shown here to be distinctive from many other xanthid larvae, and it may be a general characteristic of the genus *Micropanope* (sensu lato). This contention is supported by a nearly identical antennal configuration for zoeae of *M. barbadensis*. However, similar antennal morphological characteristics are seen in the larvae of *Paramedaeus noelensis* and *Heterozius rotundifrons*. This similarity in antennal morphology allows establishment of a separate antennal classification typed "Group E" for larvae of the Xanthidae (Gore et al. 1981). Larvae in this grouping might be considered more advanced than most xanthids, although *P. noelensis* has four zoeal stages and is otherwise similar in development to other members of the family. *Heterozius* has two zoeal stages but, as noted by Wear (1968), may not belong in the Xanthidae.

Status of *Micropanope* in Family Xanthidae

Guinot (1967) discussed systematic relationships among adults of the Xanthidae and considered the genus *Micropanope* to be a mixture of several distinct generic groups which were intermediate between the genera *Panopeus* and *Pilumnus*. She concluded *Micropanope* to be more closely related to *Panopeus* than to *Pilumnus*.

A comparison of the overall larval morphology of *M. sculptipes* with *Panopeus herbstii* and *Pilumnus dasypodus* (Table 2) reveals a much closer similarity between larvae of *M. sculptipes* and *Panopeus herbstii* than between *M. sculptipes* and *Pilumnus dasypodus*. Examination of the antennal structure for these three species shows that the length of the antennal exopodite relative to that of the antennal protopodite for *M. sculptipes* (exopodite one-sixth protopodite length) is intermediate between the advanced state seen in *Panopeus herbstii* (exopodite minute) and the primitive state seen in *Pilumnus dasypodus* (exopodite equals protopodite length), being more similar to *Panopeus herbstii*. Assuming that the antennal exopodite relative length is an indicator of the degree of relative primitiveness among xanthid species (Lebour 1928; Aikawa 1929), it can be concluded on this larval character that *Micropanope* is evolutionarily more closely related to *Panopeus* than to *Pilumnus*. This finding supports the contentions of Guinot (1967), and the apparent alliance between both larvae and adults of *Micropanope* and *Panopeus* emphasizes the importance which larval taxonomy may have in determining systematic and possible evolutionary relationships within the complex family Xanthidae.

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LITERATURE CITED

AIKAWA, H.
1929. On larval forms of some Brachyura. Rec. Oceanogr. Works Jpn. 2:17-55.
1937. Further notes on brachyuran larvae. Rec. Oceanogr. Works Jpn. 9:87-162.

CHAMBERLAIN, N. A.
1961. Studies on the larval development of *Neopanope texana sayi* (Smith) and other crabs of the family Xanthidae (Brachyura). Johns Hopkins Univ., Chesapeake Bay Inst., Tech. Rep. 22, 35 p.
1962. Ecological studies of the larval development of *Rhithropanopeus harrisii* (Xanthidae, Brachyura). Johns Hopkins Univ., Chesapeake Bay Inst., Tech. Rep. 28, 47 p.

COSTLOW, J. D., JR., AND C. G. BOOKHOUT.
1961a. The larval stages of *Panopeus herbstii* Milne-Edwards reared in the laboratory. J. Elisha Mitchell Sci. Soc. 77:33-42.
1961b. The larval development of *Eurypanopeus depressus* (Smith) under laboratory conditions. Crustaceana 2:6-15.
1966. Larval development of the crab, *Hexapanopeus angustifrons*. Chesapeake Sci. 7:148-156.
1967. The larval stages of the crab, *Neopanope packardii* (Kingsley), in the laboratory. Bull. Mar. Sci. 17:52-63.
1968. Larval development of the crab, *Leptodius agassizii* A. Milne-Edwards in the laboratory (Brachyura, Xanthidae). Crustaceana Suppl. 2:203-213.

1971. The effect of cyclic temperatures on larval development in the mud-crab *Rhithropanopeus harrisii*. *In* D. J. Crisp (editor), Fourth European Marine Biology Symposium, p. 211-220. Camb. Univ. Press, Lond.

COSTLOW, J. D., JR., C. G. BOOKHOUT, AND R. MONROE.
1962. Salinity-temperature effects on the larval development of the crab, *Panopeus herbstii* Milne-Edwards, reared in the laboratory. Physiol. Zool. 35:79-93.

GORE, R. H., C. L. VAN DOVER, AND K. A. WILSON.
1981. Studies on decapod Crustacea from the Indian River region of Florida. XX. *Micropanope barbadensis* (Rathbun, 1921): the complete larval development under laboratory conditions (Brachyura, Xanthidae). J. Crustacean Biol. 1:28-50.

GUINOT, D.
1967. Recherches preliminaires sur les groupements naturels chez les crestaces decapodes brachyoures. II. Les anciens genres *Micropanope* Stimpson et *Medaeus* Dana. Bull. Mus. Natl. Hist. Nat., 2e Ser. 39:345-374.

HYMAN, O. W.
1925. Studies on the larvae of crabs of the family Xanthidae. Proc. U.S. Natl. Mus. 67(2575), 22 p.

LEBOUR, M. V.
1928. The larval stages of the Plymouth Brachyura. Proc. Zool. Soc. Lond. 1928:473-560.

MCDONALD, H. J., AND W. LANG.
1976. The larval development of *Pilumnus sayi* Rathbun reared in the laboratory. Am. Zool. 16:219.

MCMAHAN, M. R.
1967. The larval development of *Neopanope texana texana* (Stimpson) (Xanthidae). Fla. Board Conserv. Mar. Res. Lab. Leafl. Ser. 2, 16 p.

ONG, K.-S., AND J. D. COSTLOW, JR.
1970. The effect of salinity and temperature on the larval development of the stone crab, *Menippe mercenaria* (Say), reared in the laboratory. Chesapeake Sci. 11:16-29.

PORTER, H. J.
1960. Zoeal stages of the stone crab, *Menippe mercenaria* Say. Chesapeake Sci. 1:168-177.

RATHBUN, M. J.
1930. The Cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae and Xanthidae. U.S. Natl. Mus. Bull. 152, 609 p.

SABA, M., M. TAKEDA, AND Y. NAKASONE.
1978. Larval development of *Epixanthus dentatus* (White) (Brachyura, Xanthidae). Bull. Natl. Sci. Mus. (Tokyo), Ser. A (Zool.) 4:151-161.

SANDIFER, P. A.
1974. Larval stages of the crab, *Pilumnus dasypodus* Kingsley (Crustacea, Brachyura, Xanthidae), obtained in the laboratory. Bull. Mar. Sci. 24:378-391.

SCOTTO, L. E.
1979. Larval development of the Cuban stone crab, *Menippe nodifrons* (Brachyura, Xanthidae), under laboratory conditions with notes on the status of the family Menippidae. Fish. Bull., U.S. 77:359-386.

WEAR, R. G.
1968. Life-history studies on New Zealand Brachyura. 2. Family Xanthidae. Larvae of *Heterozius rotundifrons* A. Milne-Edwards, 1867, *Ozius truncatus* H. Milne-Edwards, 1834, and *Heteropanope* (*Pilumnopeus*) *serratifrons* (Kinahan, 1856). N. Z. J. Mar. Freshwater Res. 2:293-332.
1970. Notes and bibliography on the larvae of xanthid crabs. Pac. Sci. 24:84-89.

YANG, W. T.
1967. A study of zoeal, megalopal, and early crab stages of some oxyrhynchous crabs (Crustacea: Decapoda). Ph.D. Thesis, Univ. Miami, Coral Gables, Fla., 459 p.

ESTABLISHMENT OF NONINDIGENOUS RUNS OF SPRING CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*, IN THE WIND RIVER DRAINAGE OF THE COLUMBIA RIVER, 1955-63

ROY J. WAHLE[1] AND ED CHANEY[2]

ABSTRACT

In 1955, cooperating agencies of the Columbia River Fishery Development Program embarked upon a 9-year program to introduce nonindigenous spring chinook salmon, *Oncorhynchus tshawytscha*, into Wind River, a tributary of the Columbia River. The program consisted of: 1) construction of a fishway at an impassable falls on the lower Wind River, 2) transplantation of nonindigenous adult spring chinook salmon from the Columbia River to Carson National Fish Hatchery on the upper Wind River, and 3) rearing and release of juvenile spring chinook salmon into the Wind River. As a result of these activities, approximately 66,000 adult spring chinook salmon returned to Carson hatchery during 1959-79. Additional nonindigenous adult fish annually utilized natural spawning habitat of the Wind River drainage. Hatchery and naturally produced spring chinook salmon from the Wind River contributed to marine and freshwater commercial and sports fisheries. Through 1979, about 46.5 million spring chinook salmon eggs and 3.5 million juveniles were transplanted from Carson hatchery to other areas of the Pacific Northwest.

The Columbia River Basin produces the world's largest runs of chinook salmon, *Oncorhynchus tshawytscha*, and steelhead, *Salmo gairdneri*; major runs of coho salmon, *O. kisutch*; and lesser runs of sockeye salmon, *O. nerka*, and chum salmon, *O. keta*. Since the 1938 completion of Bonneville Dam on the main-stem Columbia River at river mile 146.1 from the Pacific Ocean, the Columbia River Basin has been divided into upper and lower river fishery management units encompassing areas above and below Bonneville Dam, respectively. Chinook salmon produced in the upper river area, particularly the spring and summer runs,[3] provided the bulk of freshwater commercial catches which annually averaged approximately 29 million lb from 1866 to 1940, and peaked at more than 40 million lb/yr during 10 yr of that period (Beiningen[4]).

By the beginning of the 1940's, land and water developments in the upper Columbia Basin had eliminated or degraded major anadromous salmonid spawning and rearing areas. The resulting reduced production in combination with overfishing had a significant diminishing effect on salmon and steelhead runs originating in the upper basin (Chaney and Perry[5]).

In 1949 the U.S. Congress appropriated initial funds for a cooperative state-federal fishery development effort which soon came to be known as the Columbia River Fishery Development Program (CRFDP). This program is now administered by the Northwest Region Environmental and Technical Services Division, National Marine Fisheries Service, NOAA, Portland, Oreg. Operations are largely conducted via contract with the U.S. Fish and Wildlife Service and fishery management agencies of Oregon, Washington, and Idaho. The program has two primary components: protection and improvement of stream environments for anadromous salmonids, and hatchery production of salmon and steelhead to partially offset the loss of production from natural spawning and rearing areas.[6]

[1]Environmental and Technical Services Division, National Marine Fisheries Service, NOAA, 811 NE Oregon Street, P.O. Box 4332, Portland, OR 97209.

[2]Northwest Resource Information Center, Inc., P.O. Box 427, Eagle, ID 83616.

[3]Distinct runs of adult chinook salmon enter the Columbia River from February through October of each year. Those entering the river in late February through May are classed as spring chinook salmon. Spring chinook salmon destined for upriver spawning areas generally enter the Columbia in late March through May with peak passage at Bonneville Dam in late April or early May. Chinook salmon entering the Columbia from late May through July are classed as summer chinook salmon and are all destined for spawning areas above Bonneville Dam (Chaney and Perry see footnote 5).

[4]Beiningen, K. T. 1976. Investigative reports of Columbia River fisheries project, Section E-Fish Runs. Prepared for Pacific Northwest Regional Commission, Vancouver, Wash., 65 p.

[5]Chaney, E., and L. E. Perry. 1976. Columbia Basin salmon and steelhead analysis. Prepared for Pacific Northwest Regional Commission, Vancouver, Wash., 74 p.

[6]Program activities to date include clearing of obstructions

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In 1955, CRFDP cooperating agencies initiated a 9-yr program to introduce spring chinook salmon into Wind River, which enters the Columbia River at river mile 155 in southwestern Washington (Figure 1). Historically, chinook salmon were blocked from all but a few miles of the lower Wind River by an impassable series of falls located 3.7 mi upstream from its confluence with the Columbia River. The upper Wind River drainage was believed to contain substantial spring chinook salmon spawning and rearing habitat and to have the potential for supporting a productive spring chinook salmon hatchery program. Approximately 35,000 spring chinook salmon eggs from Camas Creek, Idaho, were transferred to Carson National Fish Hatchery on upper Wind River in 1945. About 20,500 resulting fingerlings were marked and released into the Wind River in October 1946. In 1949, 21 adult spring chinook salmon were observed below Shipperd Falls. Four carcasses bearing the 1946 mark were subsequently recovered (Zimmer et al. 1963).

This report is a summary of the 1955-63 Wind River spring chinook salmon introduction program and results through 1979.

MAJOR ELEMENTS OF THE PROGRAM

The Wind River spring chinook salmon introduction program had three discrete, interrelated elements: 1) construction of a fishway at Shipperd Falls, 2) trapping nonindigenous adult spring chinook salmon from a heterogenous population passing Bonneville Dam on the main-stem Columbia River and transporting them to hatchery facilities on the upper Wind River, and 3) holding of transported adults to maturity, spawning the adults, and rearing the resulting progeny to migrant size for release into Wind River.

from about 2,000 mi of streams, construction of 87 fishways at natural barriers, installation of 570 screens at diversion ditches and canals, and construction or modernization of 22 salmon and steelhead hatcheries and 7 rearing ponds which annually produced an average of 98 million salmon (2.6 million lb) and 2.3 million steelhead (350,000 lb) during 1971-76. Wahle and Vreeland (1978) list numerous operational improvement studies also funded to complement artificial production throughout the basin.

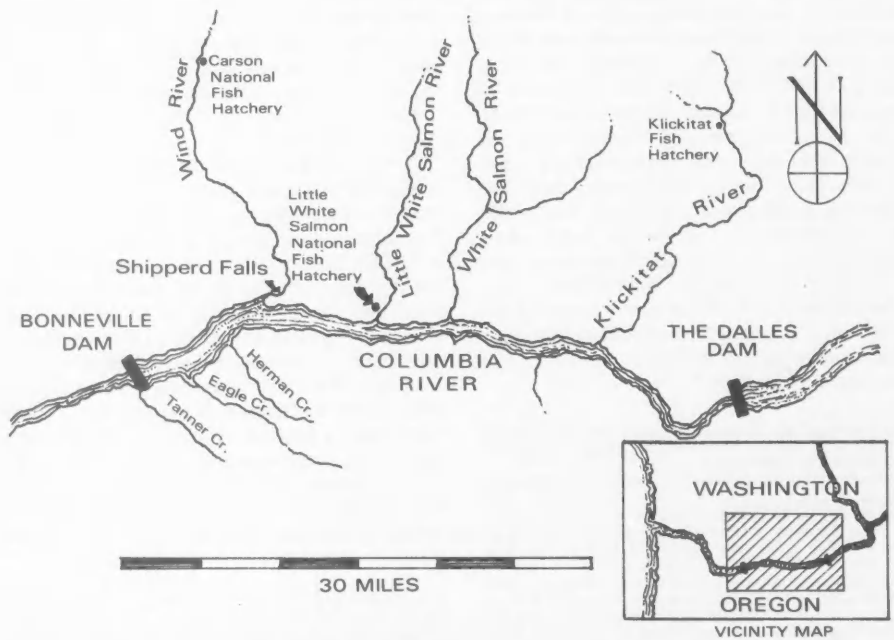

FIGURE 1.—Wind River and vicinity.

Shipperd Falls Fishway

Shipperd Falls is a series of falls ranging from 3 to 15 ft high with a collective total vertical drop of 44.8 ft. The falls are located 3.7 mi upstream from the Wind River's confluence with the Columbia River. Small numbers of steelhead reportedly were able to negotiate the falls during periods of high river flow during spring runoff (Bryant 1949). However, the falls apparently presented an impassable barrier to chinook salmon at all flows. No spring chinook salmon spawning habitat exists in the Wind River drainage below Shipperd Falls.

Construction of a fishway began in 1953 and was completed in 1956. A barrier dam was constructed across the stream to increase the height of the lowermost vertical drop of the falls to block upstream migrants and lead them to the fishway entrance. The fishway is of single slot vertical baffle design, commonly employed where integral pool regulation is not possible. Forty-five 9-ft long, 6-ft wide pools were constructed on a 1:9 slope providing 1-ft vertical rise from pool to pool. Total length of the fishway including entrance and exit facilities is about 454 ft with a vertical rise from downstream entrance to upstream exit of 44.8 ft. When complete the fishway provided fish passage at all stream flows (Figures 2, 3).

FIGURE 2.—Shipperd Falls and fishway.

FIGURE 3.—Shipperd Falls and fishway.

Adult Trapping and Hauling

At the time the Wind River spring chinook salmon introduction was initiated, artificial propagation of all salmon within the Columbia Basin was generally ineffective and virtually nonexistent for spring chinook salmon. Lacking a convenient source of nonindigenous juvenile or adult spring chinook salmon for transplantation to the Wind River, researchers decided to trap adults for brood stock from the heterogenous population passing Bonneville Dam enroute to various upriver tributary spawning areas.

A specially designed trap similar to that described by Gunsolus and Eicher[7] was installed at the fishway on the north side of Bonneville Dam. The trap basically consisted of a hopper which was lowered into the fishway to intercept and collect upstream migrants. Once several adult spring chinook salmon had entered the hopper, it was raised from the fishway, positioned over and emptied into a 1,000-gal capacity tank truck previously filled with water from the fishway (Figure 4). This process was repeated until each truck held approximately 20 adult fish. During the loading operation, water in the truck tank was continually being drawn from the fishway, circulated through the tanks, and released to the forebay of the dam. Water in the tank was mechanically aerated during the approximately 1 h transportation time to Carson Hatchery. At the hatchery, the tank trucks were emptied into adult holding ponds. The fish were retained in water throughout the trapping and hauling operation.

[7] Gunsolus, R. T., and G. J. Eicher. 1962. Evaluation of fish passage facilities at the Pelton Project on the Deschutes River in Oregon. Oregon Department of Fish and Wildlife Research and Management Laboratory, 17330 SE Evelyn St., Clackamas, OR 97015, 133 p.

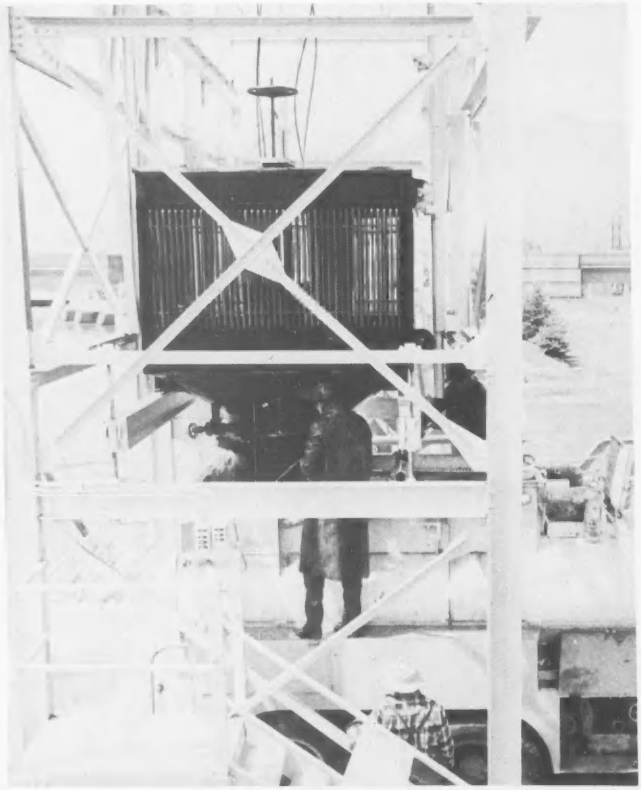

FIGURE 4.—Transfer of adult spring chinook from hopper of fishway to tank truck for transport to Carson Hatchery.

Zimmer et al. (1963) reported on adult mortalities resulting from trapping and hauling operations.

During 1955-63 a total of 4,239 adult spring chinook salmon were trapped at Bonneville Dam and hauled to Carson Hatchery. Table 1 displays trapping and related details for each year of that period.

Hatchery Operations

The adult spring chinook salmon trapped at Bonneville Dam in the spring of each year during 1955-63 were held in adult holding ponds at Carson Hatchery (Figure 5) until sexually mature and ready for spawning in late August and early September. Eggs taken were fertilized and incubated and the resulting juveniles reared for about 13 mo in hatchery raceways. Zimmer et al. (1963) provided details on hatchery facilities, water supply, fish cultural operations, disease, and diets.

During the 1955-63 transplantation program, about 8.5 million eggs were taken from adult female spring chinook salmon trapped at Bonneville Dam. In 1960-63, an additional 5.3 million eggs were taken from adult female spring chinook salmon returning to the hatchery as the result of releases of the progeny of the transplanted fish. Total juvenile releases at the hatchery from the 1955-63 brood years was about 10.6 million yearlings (Table 2).

EVALUATION OF THE RESULTS OF THE PROGRAM

Adult fish counts at Shipperd Falls fishway, returns to Carson National Fish Hatchery and

TABLE 1.—Adult spring chinook salmon trapped at Bonneville Dam and transferred to Carson National Fish Hatchery, 1955-63.

Year	Bonneville Dam spring chinook salmon count[1]	Period of trapping	No. days of trapping	Total trapping-period count[2]	Fish transferred to hatchery			
					Male[1]	Female	Total	Percent of trapping-period count
1955	171,596	19-22, 25, 27 April	6	28,007	161	356	517	1.85
1956	63,449	4-8 May	5	7,595	228	270	498	6.55
1957	136,440	22-26 April	5	8,111	192	234	426	5.25
1958	75,206	1-3, 5, 6 May	5	4,870	164	360	524	10.76
1959	61,133	27 April-1, 4, 11-15 May	11	10,740	94	90	184	1.71
1960	69,597	26 April-1 May	6	7,334	237	290	527	7.19
1961	98,695	17-22 April	6	1,993	252	293	545	27.30
1962	91,116	23-27 April, 3, 4, 7 May	8	13,067	212	267	479	3.67
1963	75,471	22-27 April	6	4,388	—	—	513	11.69

[1]Includes jacks.
[2]Washington shore fishway only.

FIGURE 5.—Carson National Fish Hatchery.

TABLE 2.—Wind River Transplantation Program, 1955-79.

Year	Number adults hauled	Shipperd Falls adult count	Carson Hatchery returns[1]	Number fingerlings released at hatchery	Brood year
1955	517	—	—	—	—
1956	498	—	—	—	—
1957	426	—	—	967,000	1955
1958	524	—	—	623,000	1956
1959	184	—	107	733,000	1957
1960	527	854	552	1,016,000	1958
1961	545	1,032	609	261,000	1959
1962	479	2,515	1,718	[2]1,479,000	1960
1963	513	1,255	825	1,265,000	1961
1964	—	5,429	2,517	3,037,000	1962
1964	—	—	—	39,000	[3]1963
1965	—	2,284	1,474	[4]1,154,000	1963
1966	—	4,174	3,666	1,909,000	1964
1967	—	—	2,749	2,412,000	1965
1968	—	—	[5]663	1,613,000	1966
1969	—	—	1,609	1,535,000	1967
1970	—	—	3,120	757,000	1968
1971	—	—	4,250	1,178,000	1969
1972	—	—	6,641	1,409,000	1970
1973	—	—	2,189	1,541,000	1971
1974	—	—	1,563	2,001,000	1972
1975	—	—	4,905	2,000,000	1973
1975	—	—	—	197,000	[3]1974
1976	—	—	5,496	2,291,000	1974
1976	—	—	—	253,000	[3]1975
1977	—	—	2,975	2,813,000	1975
1978	—	—	2,976	2,836,000	1976
1979	—	—	2,541	1,792,000	1977

[1]After a sufficient number of adults had entered hatchery holding ponds, entrance to the hatchery was frequently blocked, forcing returning adults to spawn in Wind River and tributaries.
[2]First year released juveniles included progeny of nontransplanted adults.
[3]Time of release study.
[4]Included last juveniles from transplanted fish.
[5]Last year of possible returns resulting from first generation progeny of transplanted fish.

resulting juvenile releases, and Wind River spawning ground surveys provided the primary means of evaluating results of the Wind River spring chinook salmon introduction program. Secondary indicators were the amount of contribution to catches and a surplus of eggs and juveniles available from Carson hatchery for transplantation to other areas of the Northwest.

Shipperd Falls Counts

Counting of adult upstream migrant salmonids began at Shipperd Falls fishway in 1954 and terminated in 1966. Fish ascending the fishway were trapped in a confined area of the upstream exit facility, raised near the water surface by an electrically operated false floor, identified, and counted. An adjustable headgate was then opened, allowing the fish to exit from the fishway and continue upstream.

Frequency of counting varied with the number and rate of migration of spring chinook salmon through the fishway. Counting was intermittent during 1954-58, not conducted in 1959, and conducted throughout the time of spring chinook salmon migration in 1960-66. Spring chinook salmon counts ranged from 1 fish in 1957 to 5,429 fish in 1964 (Table 2).

Hatchery Returns-Juvenile Releases

Spring chinook salmon from any given brood year returned to Carson Hatchery as 3-yr-old precocious males (jacks) and 4-, 5-, and 6-yr-old adults. Table 3 contains age composition of spring chinook salmon from the 1963-73 broods that returned to the hatchery.

The first spring chinook salmon resulting from the transplantation program returned to Carson Hatchery in 1959: 99 jacks, 6 adult males, and 2 adult females. The first significant return, 522 spring chinook salmon in 1960, consisted of 331 adult females, 170 adult males, and 51 jacks.

Transplantation of brood stock from Bonneville Dam to Carson Hatchery terminated with the completion of 1963 trapping and hauling operations. Thereafter, hatchery brood stock consisted exclusively of adult fish returning as the result of juvenile releases at the hatchery.

From 1964 through 1979, about 49,000 spring chinook salmon returned to Carson Hatchery adult holding ponds. The annual average return during that period was about 3,100 spring chinook salmon. The peak return of 6,641 occurred in 1972 (Table 2).

Table 2 displays the number of juvenile spring chinook salmon released into the Wind River at Carson Hatchery 1956-79. Releases during 1956-61 (brood years 1954-59) were exclusively progeny of fish trapped at Bonneville Dam; 1962-65 releases (brood years 1960-63) were from a composite of adults transported and those returning to the hatchery from earlier juvenile releases. The approximately 26.6 million juveniles released 1966-79 (brood years 1964-77) were all progeny of adult spring chinook salmon returning to the hatchery.

TABLE 3.—Age composition of 1967-73 broods of spring chinook salmon returning to Carson National Fish Hatchery.

Brood year	3	4	5	6	Total
1967	0	2,580	2,470	0	5,050
1968	952	4,124	1,066	261	6,403
1969	50	1,022	261	0	1,333
1970	101	905	264	24	1,294
1971	384	4,630	5,025	0	10,039
1972	10	161	46	5	222
1973	288	2,907	2,360	12	5,567
Total	1,785	16,329	11,492	302	29,908
% of total	6	55	38	1	100

Spawning Ground Surveys

Achieving the production potential of natural habitat in upper Wind River and its tributaries was the companion goal to developing a self-sustaining spring chinook salmon hatchery program at Carson Hatchery. Annual spawning ground surveys for spring chinook salmon in the Wind River and selected tributaries began in 1959. Surveys were conducted in late August and early September; Table 4 contains data on the 1959-79 surveys. The largest number of spring chinook salmon observed during that period was 1,476 fish in 1962; the largest number of redds counted in the same period was 527 in 1964. Figure 6 illustrates the general distribution of spring chinook salmon spawners in Wind River and tributaries based upon composite data from several years' surveys.

TABLE 4.—Spawning ground surveys of Wind River spring chinook salmon, 1959-79.

	Above hatchery		Below hatchery		Totals	
Year	Fish	Redds	Fish	Redds	Fish	Redds
1959	—	—	24	—	24	—
1960	34	107	6	9	40	116
1961	23	62	8	12	31	74
1962	35	155	1,441	—	1,476	155
1963	—	—	—	—	—	—
1964	579	422	107	105	686	527
1965	—	—	—	—	—	—
1966	111	63	121	48	232	111
1967	—	—	—	—	—	—
1968	—	—	—	—	—	—
1969	—	—	—	—	—	—
1970	59	138	72	73	131	211
1971	839	308	391	52	1,230	360
1972	372	112	189	51	561	163
1973	79	56	17	8	96	64
1974	37	30	7	2	44	32
1975	25	16	12	9	37	25
1976	23	13	37	12	60	25
1977	26	29	16	9	42	38
1978	40	25	41	22	81	47
1979	—	—	—	—	—	—

Catch Contribution

In 1959 the first adult spring chinook salmon adults resulting from progeny of the transplantation program returned to Wind River. Small numbers of spring chinook salmon were reported caught by steelhead fishermen in 1959-61. In 1962 a spring chinook salmon sport fishery developed in the Columbia River at the mouth of the Wind River. Based upon Washington Department of Fisheries salmon creel census data submitted voluntarily by fishermen, catches during 1964 and 1965 were estimated at 592 fish and 363 fish, respectively (Nye and Ward 1968).

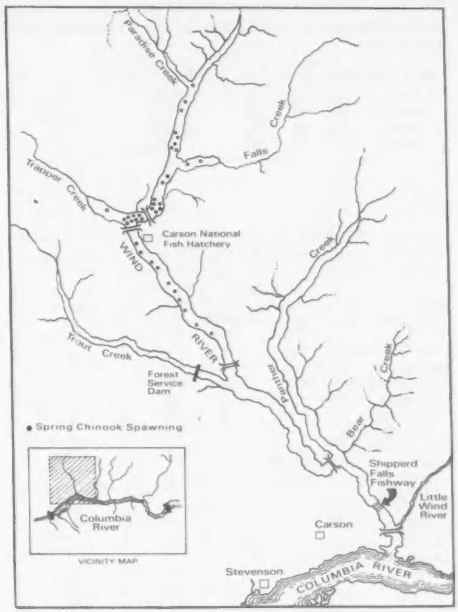

FIGURE 6.—Generalized distribution of naturally spawning chinook in the Wind River drainage. Stream widths exaggerated.

In 1966 an intensive creel census specially designed for small geographic areas[8] provided data to estimate the catch of Wind River spring chinook salmon at the confluence of the Wind and Columbia Rivers. Major features of the census program included: creel census of boat and shore fishermen twice daily 29 March-1 June, and hourly census of boat and shore fishermen for 6 weekend days and 10 weekdays, including number and species of fish caught and total hours fished. Total estimated catch for the period 29 March-1 June was 1,144 fish (Table 5). Based upon far less precise, voluntarily submitted creel census data, February-June 1964-75 Wind River spring chinook salmon sport catches ranged from 34 fish (1968) to 2,454 fish (1975) with an estimated catch of 362 spring chinook salmon in 1966 (Nye and Ward 1968; Nye et al. 1975, 1976).

[8]Donald D. Worlund, Northwest and Alaska Fisheries Center Fisheries Data and Management Systems, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

TABLE 5.—Estimates of sport catch of spring chinook salmon at the confluence of the Wind and Columbia Rivers, 29 March-1 June 1966.

Period ending	Boat	Shore	Total	Period ending	Boat	Shore	Total
17 April	69	10	79	15 May	40	28	68
24 April	269	61	330	22 May	35	7	42
1 May	271	63	334	29 May	2	1	3
8 May	239	49	288	Totals	925	219	1,144

TABLE 6.—Recovery data for marked spring chinook salmon of the 1971 brood from Carson National Fish Hatchery, 1973-76.

Area	Fishery	1973	1974	1975	1976	Total recoveries
Alaska	Troll	—	1	3	0	4
British Columbia	Troll	—	3	0	0	3
Washington:						
Cape Flattery	Troll	0	8	0	0	8
Quillayute		0	49	0	0	49
Split Rock		0	2	0	0	2
Grays Harbor		0	31	0	0	31
Columbia R.		0	17	0	10	27
Sekiu	Ocean sport	0	0	0	0	0
Neah Bay		0	9	0	0	9
LaPush		0	0	0	0	0
Westport		0	31	0	6	37
Ilwaco		12	25	0	0	37
Oregon:						
Astoria	Troll	0	2	4	0	6
Newport		0	3	0	0	3
Coos Bay		0	26	8	0	34
Bandon		0	0	1	0	1
Warrenton	Ocean sport	0	0	23	0	23
California:						
Crescent City	Troll	0	0	14	0	14
Eureka		0	15	9	0	24
	Sport	0	0	0	0	0
Columbia R.:						
Below Bonneville	Gill net	0	8	8	3	19
Above Bonneville		0	0	0	0	0
Below Bonneville	Sport	0	0	0	0	0
Above Bonneville[1]		—	—	—	—	—
Totals		12	230	70	19	331

[1]Not sampled.

In late March and early April 1972, 142,000 dorsal-right ventral marked 1970 brood Wind River spring chinook salmon juveniles were released at Carson Hatchery. From November 1971 to march 1972, 161,000 1970 brood juveniles bearing the same mark were released at two other hatcheries on nearby Klickitat and Little White Salmon Rivers. These releases were part of a Columbia River Fishery Development Program-funded marking and mark sampling program involving all spring chinook salmon rearing facilities in the Columbia River Basin. During 1972 and 1973, marks were sampled only at Washington, Oregon, and California ports. Beginning in 1974, the sampling program covered all significant Pacific coast marine and Columbia River recreational and commercial chinook salmon ports of landing from Pelican, Alaska, to Monterey, Calif. Sampling a total of 140 Wind-Klickitat-Little White Salmon-River marks, recoveries included Alaska 4, British Columbia 6, Washington 27, and California 5. Seventy-two marks were recovered in the main-stem Columbia River sport fishery and 26 in the main-stem Columbia River gill net commercial fishery.

In late March and early April 1973, about 142,000 1971 brood spring chinook salmon juveniles (average length 5½ in) bearing a distinctive adipose-right ventral mark were released from Carson Hatchery into Wind River. Table 6 contains 1973-76 mark recoveries in marine and Columbia River fisheries.

Wind River Spring Chinook Salmon Transfers

As a result of the Wind River spring chinook salmon introduction program, Carson National Fish Hatchery has become an important source of spring chinook salmon for transplantation to diverse areas within and outside the Columbia River Basin. About 46.5 million eggs and 3.5 million juveniles from adult returns to the hatchery were transferred to other areas during 1960-79 (Table 7).

These transfers contributed to the establishment of several spring chinook salmon runs, including hatchery runs to Leavenworth National Fish Hatchery on Washington's Icicle River, a tributary of the Wenatchee River, and to the Little White Salmon National Fish Hatchery on Washington's Little White Salmon River; naturally spawning runs were created in Fall Creek, tributary to Oregon's Willamette River, and in the Selway River, tributary to the Clearwater River in Idaho.

SUMMARY

In 1955, a 9-yr program was initiated to introduce nonindigenous spring chinook salmon into Wind River, a southwestern Washington tributary of the Columbia River. A fishway was constructed to provide chinook salmon passage over a heretofore impassable falls located at Wind River mile 3.7. During 1955-63, 4,239 adult spring chinook salmon were trapped from the heterogenous population passing over Bonneville Dam

TABLE 7.—Spring chinook salmon, eggs, and juveniles by brood year transported from Carson National Fish Hatchery, 1960-79.

Year	Transferred to	Number		Brood year
		Eggs	Juveniles	
1960	Klickitat Hatchery, Wash. (W.D.F.)[1]	35,000	—	1960
1961	Klickitat Hatchery	100,000	—	1961
1961	Warm Springs Creek, Oreg. (Warm Springs Indian Tribe)	—	75,313	1960
1961	Clearwater River, Idaho (I.F.&G.)	705,711	—	1961
1962	Klickitat Hatchery	899,339	—	1962
1962	Clearwater River	959,200	—	1962
1963	Clearwater River	1,000,000	—	1963
1964	Clearwater River	1,900,000	—	1964
1964	Klickitat Hatchery	121,500	—	1964
1965	Willard N.F.H.,[2] Wash. (U.S.F.&W.)	19,341	—	1965
1965	Clearwater River	634,942	—	1965
1966	Nat'l. Marine Fisheries Service, Seattle, Wash.	—	10,000 (50-70/lb)	1966
1966	Clearwater River	—	1,018,200 (50-70/lb)	1966
1967	Clearwater River	—	1,016,300 (50-70/lb)	1967
1968	Clearwater River	—	951,970 (50-70/lb)	1968
1966	Weyerhauser Corp., Oreg.	—	10,880 (125/lb)	1966
1968	Little White Salmon N.F.H., Wash. (U.S.F.&W.)	101,000	—	1968
1969	Kooskia N.F.H., Idaho (U.S.F.&W.)	255,300	—	1969
1969	Clearwater River	990,117	—	1969
1969	Warm Springs Creek	300,017	—	1969
1970	Little White Salmon N.F.H.	1,123,190	—	1970
1970	Leavenworth N.F.H., Wash. (U.S.F.&W.)	307,810	—	1970
1970	Willamette River, Oreg. (F.C.O.)	2,999,130	—	1970
1970	Willamette River	—	359,280 (462/lb)	1970
1971	Kooskia N.F.H.	1,532,020	—	1971
1971	Leavenworth N.F.H.	600,000	—	1971
1971	Southeast Alaska (A.F.&G.)	500,000	—	1971
1971	Clearwater River	2,423,080	—	1971
1972	Southeast Alaska	1,510,000	—	1972
1972	Leavenworth N.F.H.	600,860	—	1972
1972	Klickitat Hatchery	5,495,160	—	1972
1972	Willamette River	1,730,760	—	1972
1972	Little White Salmon N.F.H.	1,070,610	—	1972
1972	Kooskia N.F.H.	801,890	—	1972
1973	Little White Salmon N.F.H.	846,640	—	1973
1973	Eagle Creek N.F.H., Oreg. (U.S.F.&W.)	354,000	—	1973
1973	Leavenworth N.F.H.	747,000	—	1973
1974	Abernathy N.F.H., Oreg. (U.S.F.&W.)	113,000	—	1974
1974	Little White Salmon N.F.H.	300,000	—	1974
1975	Entiat N.F.H., Wash. (U.S.F.&W.)	1,000,000	—	1975
1975	Leavenworth N.F.H.	1,056,000	—	1975
1975	Leavenworth N.F.H.	1,243,000	—	1975
1975	Kooskia N.F.H.	300,000	—	1975
1975	Klickitat Hatchery	449,000	—	1975
1976	Kooskia N.F.H.	1,000,000	—	1976
1976	Entiat N.F.H.	721,000	—	1976
1976	Leavenworth N.F.H.	2,443,000	—	1976
1976	Winthrop N.F.H., Wash. (U.S.F.&W.)	473,000	—	1976
1976	Marion Forks Hatchery, Oreg. (F.C.O.)	744,000	—	1976
1977	Leavenworth N.F.H.	721,000	—	1977
1977	Leavenworth N.F.H.	1,171,000	—	1977
1978	Leavenworth N.F.H.	2,043,000	—	1978
1978	Leavenworth N.F.H.	250,000	—	1978
1979	Leavenworth N.F.H.	2,238,000	—	1979
1979	Leavenworth N.F.H.	315,000	—	1979
1979	Kooskia N.F.H.	200,000	—	1979
	Totals	46,543,617	3,441,943	

[1]Abbreviations: (W.D.F.) Washington Department of Fisheries, (I.F.&G.) Idaho Fish and Game Department, (U.S.F.&W.) U.S. Fish and Wildlife Service, (F.C.O.) Fish Commission of Oregon.
[2]N.F.H. - National Fish Hatchery.

at Columbia River mile 146.1 and transferred to Carson National Fish Hatchery on the upper Wind River. About 10.6 million yearling progeny of these fish were released into Wind River.

From 1959 to 1979, about 66,000 adult spring chinook salmon returned to Carson Hatchery. During that period about 37 million yearling progeny of the 1955-77 broods were released into Wind River. Surveys of natural spawning grounds during 1959-78 recorded a peak number of 1,476 spring chinook salmon in 1962 and 527 redds in 1964. A spring chinook salmon sport fishery developed within the Wind River drainage and at its confluence with the Columbia River at the mouth of the Wind. Marking and mark sampling programs indicated Wind River spring chinook

salmon contributed to marine commercial and recreational fisheries from Alaska to California, and to main-stem Columbia River fisheries. During 1960-79, about 46.5 million eggs and 3.5 million juveniles from spring chinook salmon introduced to Wind River were transplanted to other Pacific Northwest locations.

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LITERATURE CITED

BRYANT, F. G.
1949. A survey of the Columbia River and its tributaries with special reference to its fishery resources. 2. Washington streams from the mouth of the Columbia River to and including the Klickitat River (Area 1). U.S. Fish Wildl. Serv., Spec. Sci. Rep. 62, 110 p.

NYE, G. D., AND W. D. WARD.
[1968.] Washington salmon sport catch report from punch card returns in 1967. Wash. Dep. Fish., Olympia, 39 p.
[1974.] Washington salmon sport catch report from punch card returns in 1973. Wash. Dep. Fish., Olympia, 50 p.

NYE, G. D., W. D. WARD, AND L. J. HOINES.
[1975.] Washington State salmon sport catch report, 1974. Wash. Dep. Fish., Olympia, 49 p.
[1976.] Washington State sport catch report, 1975. Wash. Dep. Fish., Olympia, 58 p.

WAHLE, R. J., AND R. R. VREELAND.
1978. Bioeconomic contribution of Columbia River hatchery fall chinook salmon, 1961 through 1964 broods, to the Pacific salmon fisheries. Fish. Bull., U.S. 76:179-208.

ZIMMER, P. D., R. J. WAHLE, AND E. M. MALTZEFF.
1963. Progress report spring chinook transplantation study, 1955-61. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 443, 24 p.

ESTIMATED GROWTH OF SURFACE-SCHOOLING SKIPJACK TUNA, *KATSUWONUS PELAMIS*, AND YELLOWFIN TUNA, *THUNNUS ALBACARES*, FROM THE PAPUA NEW GUINEA REGION

J. W. J. WAŃKOWSKI[1]

ABSTRACT

The study was undertaken on length-frequency data collected from the Papua New Guinea pole-and-line fishery between June 1977 and December 1979.

Both skipjack and yellowfin tunas are recruited to all areas of the fishery at between 30 and 46 cm fork length. Skipjack tuna remain in the exploited phase up to an average 69 cm fork length and yellowfin tuna up to an average 85 cm fork length. Periods of time during which the greatest range of fork length occurred in the catch correspond with periods of low abundance, as inferred from catch per unit of effort indices. The estimated von Bertalanffy parameters are $k = 0.0429$ and $L_\infty = 74.8$ cm for skipjack tuna; and $k = 0.0243$ and $L_\infty = 180.9$ cm for yellowfin tuna (k on a monthly basis). Estimated growth over the observed range of modal values corresponds closely with that estimated from Papua New Guinea tagging data for skipjack tuna and from studies in other regions for yellowfin tuna.

Modal progressions indicate a 12-month periodicity in mass movement of yellowfin tuna stocks in northerly and southerly directions. The presence of two skipjack tuna spawning groups, one spawning during the northern summer and the other during the northern winter, is indicated by back calculation to date of birth of all length-frequency modes using an estimate of growth derived from the tag and recapture data.

With the recent expansion of surface fisheries for skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*, in the Pacific (Bour and Galenon 1979; Kearney[2]) the need for information on this resource is becoming increasingly important for rational management. One method that might provide the quantitative information necessary is that of estimating yield per recruit (Schaefer and Beverton 1963), for which an estimate of growth is necessary.

Three techniques of obtaining growth estimates are in common use: the analysis of tag and recapture data, the analysis of data from the examination of hard parts of the fish for growth marks, and the analysis of modal progressions in length-frequency distributions. All three techniques have been used, with varying success, throughout the world for both yellowfin and skipjack tunas. The results of these studies have recently been reviewed by Le Guen and Sakagawa (1973) and Josse et al. (1979). Both studies recalculated published growth estimates using standardized procedures and indicated that, since the variances of the estimates were so wide, calculated growth rates for each species were not dissimilar among geographical areas.

Studies of growth of tunas in the western Pacific have been few. Yabuta et al. (1960) investigated growth of longline-caught yellowfin tuna, Lewis[3] reported the results of aging studies of skipjack tuna using readings of "daily" growth increments on otoliths, and Josse et al. (1979) analyzed skipjack tuna growth from the results of tagging studies conducted in Papua New Guinea in 1971-74.

This paper presents the results of a program of length-frequency data collection carried out from June 1977 through December 1979 from the pole-and-line (baitboat) fishery operating in Papua New Guinea waters. The results are presented as length-frequency modal progressions from which an estimate of growth is compared with estimates available from published sources. Since the

[1]Kanudi Fisheries Research Laboratory, Department of Primary Industry, P.O. Box 2417, Konedobu, Papua New Guinea; present address: Ministry for Conservation, Marine Science Laboratories, P.O. Box 114, Queenscliff, Victoria 3225, Australia.

[2]Kearney, R. E. 1979. An overview of recent changes in the fisheries for highly migratory species in the western Pacific Ocean and projections on future developments. South Pac. Bur. Econ. Co-op., Fiji, SPEC (79)17, 99 p.

[3]Lewis, A. D. 1976. The relevance of data collected in Papua New Guinea to skipjack studies in the western Pacific. Unpubl. manuscr., 5 p. Kanudi Fisheries Research Laboratory, P.O. Box 2417, Konedobu, Papua New Guinea.

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fishery takes place on several adjacent fishing grounds, and length-frequency data are available separately for each ground, the movements of groups of fish through the fishery are investigated where possible. Finally the availability of an independent estimate of skipjack tuna growth, from the tagging data, makes possible the calculation of probable date of birth of the fish comprising each modal group, the results of which indicate possible stock structure in the Papua New Guinea region.

DATA COLLECTION

Although skipjack and yellowfin tunas are found throughout Papua New Guinea waters, the fishery (Figure 1) is centered on baiting grounds on the north coast of Manus Island, within the extensive lagoon systems around and to the east of the island of New Hanover, and in the barrier reef lagoons on the northwest coast of the large island of New Britain. During the period of the present study, these four areas were effectively separated on both a fishing fleet and geographical basis. Fleet A operated in the eastern Bismarck Sea (area 4, Figure 1), fleet B operated throughout both New Hanover fishing areas (2 and 3), and fleet C also operated from New Hanover, but at any one time fished either north (area 2) or south (area 3) of the baiting grounds. The Manus-based fishery (area 1) was exploited only occasionally and by few vessels.

Fifty-one Okinawan-type vessels (Tomiyama and Hibiya 1976) operated throughout the fishery in 1977, 47 in 1978, and 41 in 1979. Poor fishing conditions caused by the northwest monsoon season from December through February preclude intensive fishing in these areas, resulting in limited data being available for this period each year.

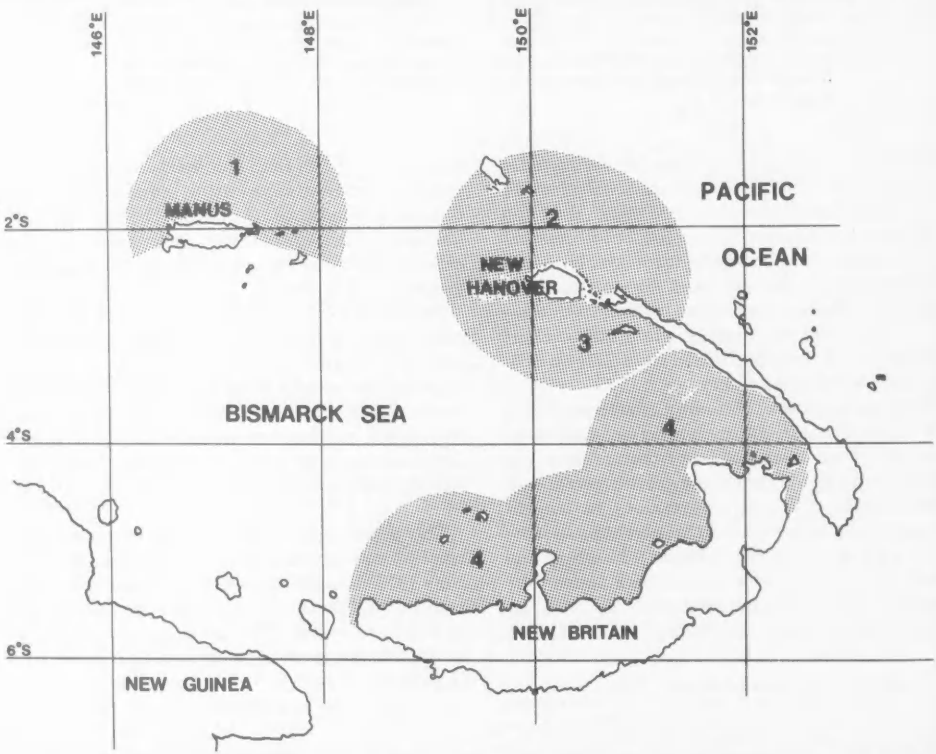

FIGURE 1.—Pole-and-line tuna fishing areas in the Papua New Guinea region (shaded): 1—north of Manus Island, 2—north of New Hanover Island, 3—south of New Hanover Island, 4—eastern Bismarck Sea.

Over the period of the study, 9.97% of the total catch consisted of yellowfin tuna, 89.83% skipjack tuna, and the remaining 0.20% other tunas and tunalike species. However, it should be noted that the proportion of yellowfin tuna in the catch is quite variable (Wańkowski 1980). The fishery since its inception in 1970 is described by Wańkowski (1980) while the 1978 and 1979 seasons are described in detail in Anonymous.[4, 5]

All vessels catch bait each day and the return to the baiting grounds is almost always accompanied by unloading the day's tuna catch onto one of the five motherships from which the fleets operate. From March 1978, length-frequency data were collected every day from each fishing area during unloading. The fork lengths (FL) of a sample of 10 skipjack and 5 yellowfin tunas from each vessel were measured to the nearest centimeter. This sample size was chosen since it represented an acceptable compromise between statistical and logistic requirements. The measurement of more than 15 fish/vessel proved impossible during busy periods of unloading, and it was considered more important to collect data from as large a number of vessels as possible than to increase sample size. Yellowfin tuna were measured only when sufficient numbers were present in individual catches to enable easy sampling, since the catches are rarely sorted by species.

During 1977, samples were measured on an ad hoc basis by Papua New Guinea Fisheries Division personnel during the course of their normal duties on board fleets operating in the Manus and eastern Bismarck Sea areas. The New Hanover fishery was sampled on a daily basis, but each sample was obtained from a small proportion of the total catch transhipped to a shore-based processing plant. It was therefore not possible in 1977 to differentiate between fish caught north or south of New Hanover.

During the 2½ yr of study, 106,933 skipjack tuna and 47,405 yellowfin tuna were measured.

DATA ANALYSIS

The length-frequency data were analyzed by area on a monthly basis. Individual monthly histograms were plotted by 1.0 cm FL interval for each of the four areas designated in Figure 1 and for the New Hanover area as a whole (areas 2 and 3, Figure 1). The separate data for north and south of New Hanover (areas 2 and 3, respectively) were obtained from fleet C only, while those for the New Hanover area as a whole were obtained only from fleet B. Monthly length-frequency distributions were therefore available separately for the Manus, New Hanover, and eastern Bismarck Sea areas.

Polymodal distributions were divided into successive unimodal distributions, using the method of "successive maxima" (Daget and Le Guen 1975). This method does not require the assumption of normality of distributions, but merely their symmetry in relation to the modal value. For samples with only one prominent mode and for the unimodal distributions resulting from the above analysis, the midpoint of the fork length interval of maximum frequency was taken as the modal length. Examples of length-frequency distributions and the resultant modal fork lengths are shown in Figure 2. Two conditions were attached to mode selection. The first was that model fork lengths were considered separate only if the midpoints of adjacent length intervals of maximum frequency were themselves separated by intervals of 3.0 cm or more. The second was that isolated peaks of only one 1.0 cm interval were not taken to represent modes (e.g., Figure 2: 1979, month 5, 61 cm).

Modal lengths were derived from all monthly samples where $n > 30$ fish (Figures 3, 4). However mean size of these monthly samples was 1,215 skipjack tuna and 578 yellowfin tuna. Only 19 (of 88) monthly skipjack tuna samples contained <400 fish and 1 <99; similarly, 21 (of 82) monthly yellowfin tuna samples contained <200 fish and 2 <49.

Because of the apparent large-scale migration between the relatively closely associated fishing areas, it was not possible to consider the results independently for each area. A serial succession of increasing modal lengths with time was designated a single group of fish distinguishable from other groups on the basis of size and progression with age. The progression which appeared to be most logical was used without taking into account the relative strength of each mode, major and minor modes being treated equally. As can be seen from Figures 3 and 4, the data does not naturally fall into conventional year-class or cohort structure. This absence of structural form, other than

[4]Anonymous. 1979. Fisheries research annual report for 1978. Dep. Primary Ind., Port Moresby, Papua New Guinea, 98 p.

[5]Anonymous. 1980. Fisheries research annual report for 1979. Dep. Primary Ind., Port Moresby, Papua New Guinea, 103 p.

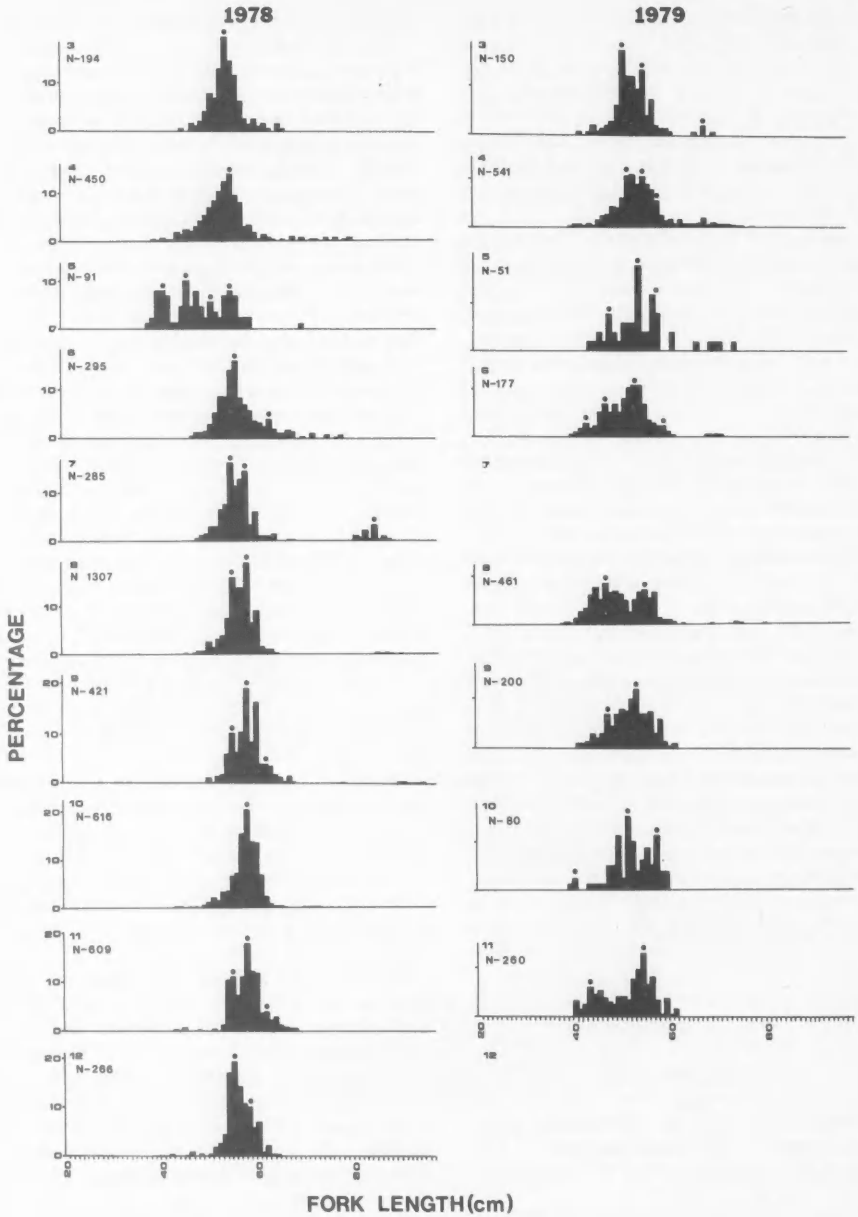

FIGURE 2.—Monthly length-frequency distributions of yellowfin tuna samples from the Papua New Guinea region from north of New Hanover (area 2) during 1978 and 1979. Modal fork lengths are indicated by dots. Note that data for July (month 7) and December (month 12) 1979 were not available.

modal progression, occurs whether the data are analyzed using all the modes as shown, or using the major mode of each monthly distribution only.

The von Bertalanffy growth function (Bertalanffy 1960) was used to describe growth. This function is usually expressed as

$$L_t = L_\infty [1 - \exp - k(t - t_0)]$$

where L_t = length at age t, L_∞ = asymptotic length, k = coefficient describing the rate of growth, and t_0 = theoretical age where L_t is zero. The Fabens' (1965) least squares procedure can be used to fit length data to the von Bertalanffy function, which then takes the form:

$$L_{t+\Delta t} = L_t + (L_\infty - L_t)(1 - \exp - k).$$

Although originally devised to fit tag return data, this procedure is equally applicable to length observations of untagged fish, and is especially useful since length at known age is not required. This procedure has been used by Rothschild (1967) and Joseph and Calkins (1969) to estimate growth of skipjack tuna from tagging data, and Le Guen and Sakagawa (1973) to estimate growth of yellowfin tuna from modal progression data.

In the present study, Fabens' (1965) procedure was used with monthly modal length data for individual groups of fish of unknown age. Estimates of L_∞ in centimeters and of k on a monthly basis were derived. Length-at-age information from published sources was used to fix the derived growth functions on a known time scale.

RESULTS

Recruitment and Exploited Size Range

Recruitment in this report refers to first entry into the fishery. Size at recruitment, as inferred from length-frequency samples, and the size range of both skipjack and yellowfin tunas exploited by the fishery varied throughout the duration of the study. The smallest size of fish of either species occurring in monthly samples was between 30 and 46 cm FL (Table 1), with the exception of a few yellowfin tuna <30 cm FL in July 1979. Skipjack tuna <46 cm and yellowfin tuna <54 cm FL were absent in February 1979. The maximum lengths of skipjack and yellowfin tunas were 74 and 96 cm FL, respectively (Table 1, Figure 5). However, few samples contained fish >69 and >85 cm FL, respectively. There were no consistent differences in size at recruitment, or in the size range exploited, among the four fishing areas.

TABLE 1.—Fork length range (centimeters) of skipjack and yellowfin tunas from all areas of the Papua New Guinea region combined, and corresponding catch per unit effort (CPUE) (metric tons per boat fishing day) and effort (number of fishing days). The fishing effort remained fairly constant from April to November of each year.

		Skipjack tuna		Yellowfin tuna		
Year	Month	Size range	CPUE	Size range	CPUE	Effort
1977	June	44-64	2.3		0.3	1,076
	July	43-65	3.0	39-92	.2	1,070
	Aug.	40-67	3.4	36-82	.4	1,093
	Sept.	38-65	1.7	37-80	.4	957
	Oct.	37-68	1.4	42-80	.4	966
	Nov.	36-68	1.7	36-77	.5	945
	Dec.	40-64	1.7	38-80	.6	579
1978	Mar.	31-69	2.2	41-80	1.4	471
	Apr.	33-69	2.4	30-80	.5	820
	May	33-69	4.6	35-81	.2	1,129
	June	40-69	4.4	34-81	.2	1,150
	July	43-69	4.4	41-88	.1	1,166
	Aug.	42-69	5.8	44-90	.3	1,168
	Sept.	40-69	6.1	46-96	.2	1,069
	Oct.	39-69	5.0	40-80	.3	1,271
	Nov.	42-68	5.0	31-80	.4	1,161
	Dec.	40-67	4.2	37-77	.4	423
1979	Feb.	46-59	5.0	54-72	.5	206
	Mar.	40-66	4.3	42-78	.4	351
	Apr.	34-65	5.5	40-78	.2	797
	May	33-68	3.3	35-80	.4	956
	June	40-70	3.5	32-83	.4	1,016
	July	40-74	2.9	24-83	.4	1,041
	Aug.	34-69	2.7	30-87	.2	922
	Sept.	33-69	2.0	31-84	.4	902
	Oct.	30-70	1.0	33-80	.6	719
	Nov.	30-70	1.1	31-90	.2	739
	Dec.	32-67	1.1	31-90	.4	276

Size at recruitment for yellowfin tuna was smaller than has been reported in the past for the eastern Pacific (Hennemuth 1961; Davidoff 1963; Anonymous[6,7]) or eastern Atlantic (Le Guen and Sakagawa 1973), where recruits are reportedly 40-60 cm and 60 cm FL, respectively, but similar to that recently reported for the eastern Pacific (Anonymous footnote 7) and for the western Indian Ocean (Marcille and Stequert 1976a). A similarity between skipjack tuna size at first recruitment in the western Pacific and western Indian Oceans is also apparent from a comparison of the results of the present study with those of Marcille and Stequert (1976b).

Suzuki (1971), Kikawa and Warashina (1972), Le Guen and Sakagawa (1973), Marcille and Stequert (1976b), and others have noted the extreme size-specificity of pole-and-line catches. In

[6]Anonymous. 1975. Annual report of the Inter-American Tropical Tuna Commission, 1974. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., La Jolla, Calif., 169 p.

[7]Anonymous. 1980. Annual report of the Inter-American Tropical Tuna Commission, 1979. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., La Jolla, Calif., 227 p.

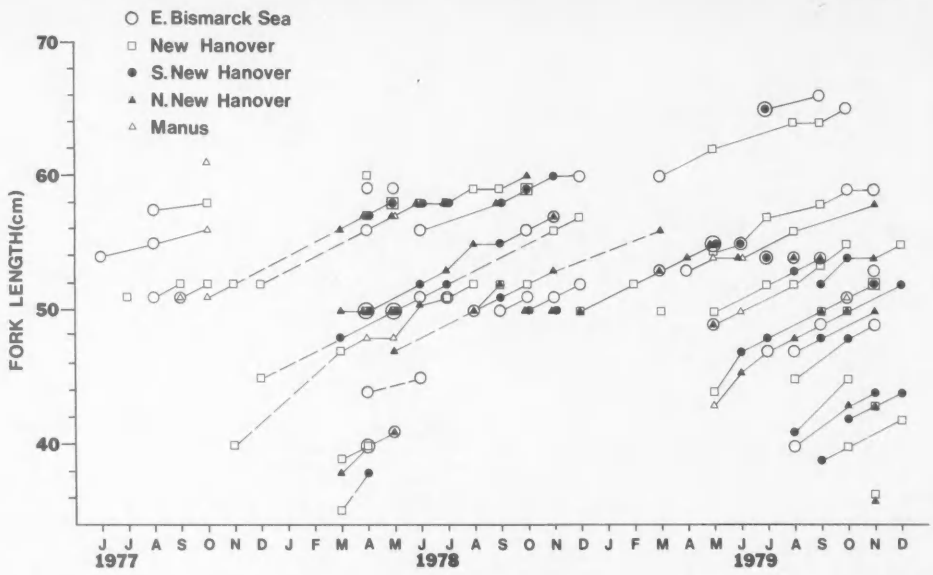

FIGURE 3.—Modal fork lengths of samples of skipjack tuna from all Papua New Guinea areas as a function of time (in months). Modal progressions are indicated by lines.

the Papua New Guinea fishery, observations have shown that vessels continually pursue and fish an individual school during periods of low catch per unit of effort (CPUE), thereby fishing few schools each day. However, during periods of high CPUE, vessels fish a large number of schools, taking fish from each school until they "go off the bite" and then moving on to a fresh school. Size-specificity of the catch, as a consequence of the fishing strategy adopted, would therefore be expected to be greatest during periods of high CPUE, vessels taking only a restricted size range of fish from each school (presumably those size classes most vulnerable to this method of fishing), and lowest during periods of low CPUE, during which a wider range of size classes would be represented in the catch.

Figures 3 and 4 show two periods, November 1977 to May 1978 and May 1979 through to the end of sampling in December 1979, during which a wide range of size classes appeared in the samples. These periods coincide with periods of relatively low skipjack tuna CPUE (Table 1). The situation is less clear for yellowfin tuna. However, since skipjack tuna composed 90% of the total catch on average, it is clear that skipjack tuna abundance would determine the adoption of a particular fishing strategy. This would therefore account for the yellowfin tuna size range, varying synchronously with that of skipjack tuna (Figures 3, 4), but independently of yellowfin tuna abundance (Table 1).

Observations from the fishing vessels during the course of the study confirmed that yellowfin tuna larger than the maximum size taken by the fishery and schools of very small skipjack tuna, both normally comparatively rare, were common throughout the fishery during late 1977 and from August to November 1979. There is therefore some indication that fishing strategy, determined by low apparent abundance, may not alone account for the appearance of small and large fish in the catch during these periods.

The results show that the timing of recruitment cannot be determined from the size composition of the landed catch. However, Ueyanagi (1970), Nishikawa et al. (1978), and Naganuma (1979) have demonstrated that skipjack tuna spawn throughout the year in the western Pacific, although in different geographical areas depending on season: a situation likely to result in continuous recruitment to the equatorial region. The re-

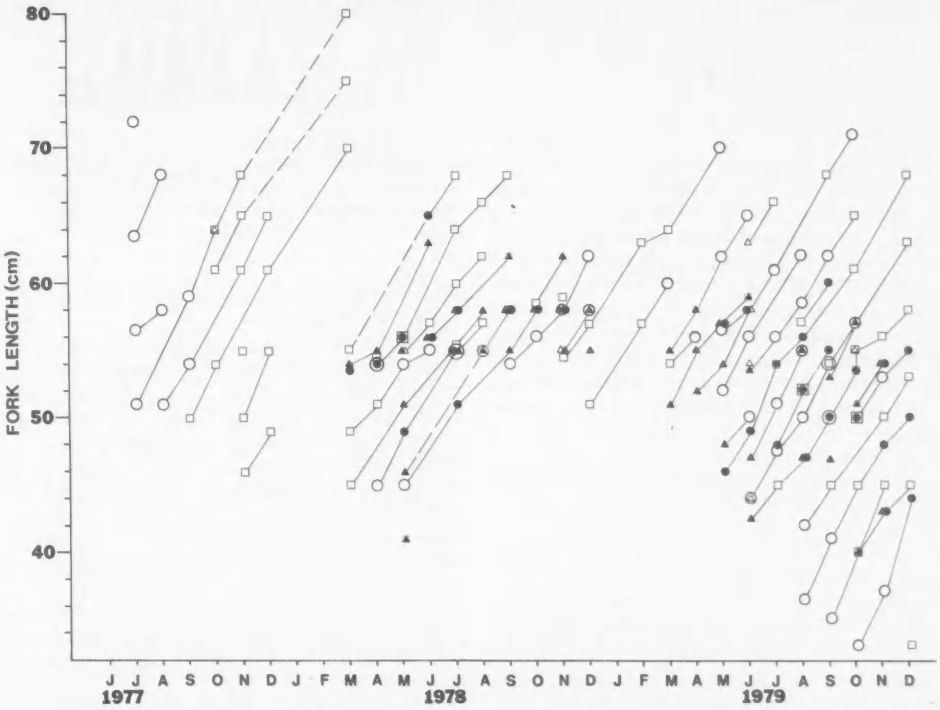

FIGURE 4.—Modal fork lengths of samples of yellowfin tuna from all Papua New Guinea areas as a function of time (in months). Modal progressions are indicated by lines. See Figure 3 for explanation of symbols.

sults of tagging studies in Papua New Guinea (Lewis 1980a, b, see footnote 8) indicate that skipjack tuna recruitment may be intermittent, and possibly dependent on periodic influxes from north and east of the area.

It has been suggested (Lewis 1980a, b, footnote 3; Anonymous[9]) that there are at least three partially mixing components to the skipjack tuna population in the western Pacific: one ranging from Japanese waters to the Equator, one centered on the Bismarck Sea and ranging to lat. 10° N, and the last extending south from the Bismarck Sea; and that these components are composed of separate spawning units, distinguishable on the basis of spawning periodicity with respect to northern and southern summers. The following analysis of data from the present study provides further evidence supporting this view.

Josse et al.'s (1979) estimates of the von Bertalanffy parameters (k = 0.94512 on an annual basis and L_∞ = 65.47 cm) for tagged skipjack tuna in the Papua New Guinea region were applied to the length-frequency modal data to estimate the dates of birth from all modal lengths available for skipjack tuna samples from the four areas. Josse et al.'s estimate is independent of the modal data, being derived from an earlier study using a different technique, and for this reason it is preferable (for present purposes) to the estimate derived in this report.

The frequency distribution of dates of birth is shown in Figure 6. The extremes of the range (pre-1975 and post-1977) are poorly represented; however, a 6-mo periodicity is indicated. Although

[8]Lewis, A. D. 1977. Tuna tagging in Papua New Guinea. Harvest, Papua New Guinea 4:13-17.

[9]Anonymous. 1976. Ad-hoc meeting of scientists to discuss skipjack fisheries developments and research requirements. Rep. meet., South Pac. Comm., Noumea, New Caledonia, 6-10 Dec. 1976, 27 p.

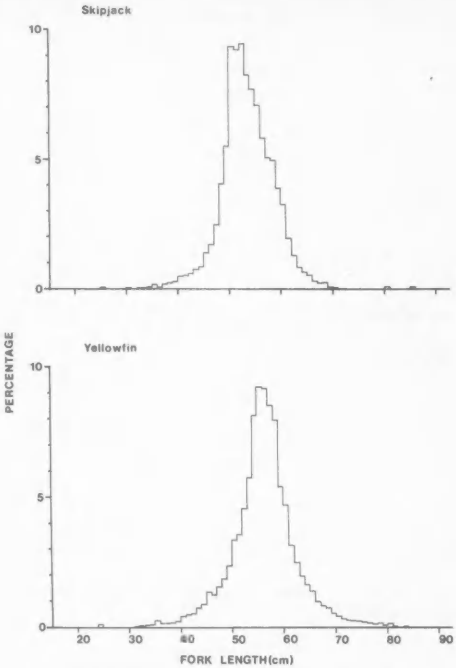

FIGURE 5.—Fork length-frequency distributions for skipjack (top) and yellowfin tunas (bottom) sampled during the study. Individual samples have been pooled for the four study areas in the Papua New Guinea region.

correspondence between 6-mo intervals and calculated peaks is not precise, considering the underlying assumption that all modal groups grew at identical rates, the observed correspondence is fairly good. The results indicate that the skipjack tuna stocks exploited by the Papua New Guinea fishery may exhibit two peaks in spawning activity, 6 mo apart.

Naganuma (1979), using gonad indices of skipjack tuna caught in the western Pacific, demonstrated the existence of two spawning groups: one spawning in southern waters in the southern summer (October-March) and the other in northern waters in the northern summer. Data for larval abundance in Papua New Guinea waters (Nishikawa et al. 1978) indicate almost identical peaks in spawning periodicity, although much continuous spawning in equatorial waters is also indicated. Spawning periodicity as determined from gonad indices and larval distribution there-

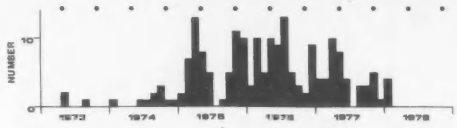

FIGURE 6.—Distribution of month of birth of skipjack tuna from the Papua New Guinea fishery calculated by the von Bertalanffy growth function, using an independent estimate of growth for all modal fork length data. Distribution is shown in one-tenths of 1 yr. Dots indicate 6-mo intervals.

fore corresponds to that determined from the results of the present study.

However, as is clear from the skipjack tuna modal data (Figure 3) and abundance (as inferred from skipjack tuna CPUE, Table 1), this possible 6-mo spawning periodicity did not result in semestral recruitment to the fishery in 1977-79. Lewis (1980a), however, reported that there were two groups of skipjack tuna present in the Bismarck Sea in 1972, apparently resulting from two periods of recruitment 6 mo or more apart. As 1972 was a year in which skipjack tuna abundance was exceedingly low, it might be expected that the consequences of possible large-scale periodic recruitment to the fishery would be more obvious then than during periods of relatively high abundance, as during the present study.

Yellowfin tuna show restricted spawning periods and semestral recruitment in many fisheries (Hennemuth 1961; Davidoff 1963; Matsumoto 1966; Le Guen et al. 1969; Richards 1969; Le Guen and Sakagawa 1973). That this is unlikely to have occurred in equatorial western Pacific waters during the period of the study is clear from Figure 4; the fairly continuous production of fish implied by the large number of modal groups passing through the fishery is unlikely to be the result of one or two short spawning periods. Although differential growth between elements resulting from a protracted spawning period might result in the observed spread in recruitment, the youth of the fish, as inferred from rate of growth estimates (Le Guen and Sakagawa 1973; present paper), would necessitate either early separation into groups of fish exhibiting different rates of growth or protracted spawning periods (perhaps continuous spawning activity).

Most identifiable groups of yellowfin tuna disappeared from the pole-and-line catch at between 62 and 71 cm FL (Figure 4). Kikawa and Warashina (1972) pointed out that the Japanese

long-range pole-and-line fisheries in the equatorial western Pacific take fish 30-100 cm FL (but mainly <70 cm), harvested well before they enter the deeper water longline fishery that exploits fish mainly >100 cm FL.

However, Wright (1980) indicated that a proportion of Japanese longline catches consist of yellowfin tuna of 70-100 cm FL which are discarded on capture owing to their unsuitability for the sashimi (raw fish) market that this fishery supplies. The equatorial western Pacific purse seine fishery exploits fish from 30 to 100 cm FL (Kikawa and Warashina 1972; Wańkowski and Witcombe[10]), about half the catch consisting of fish <100 cm. The absence of significant numbers of yellowfin tuna >70 cm in the Papua New Guinea pole-and-line catch (Figure 5) therefore indicates selectivity for smaller fish (confirmed by the absence of suitable gear, on Papua New Guinea-based vessels, for poling larger fish on board) and possible recruitment of 70-100 cm size class from the surface fishery into the longline fishery (yellowfin tuna in this region presumably spending less time at the surface with increasing age). However, that this size class of yellowfin tuna does not wholly enter deeper waters is indicated by observations of their presence in surface schools in late 1977 and late 1979, and by the fact that Japanese longliners set shallow lines when their target species is yellowfin tuna (Wright[11]).

A similar point of note is the low incidence of skipjack tuna >65 cm FL (Figure 5) in the catch. This is in contrast to the situation in the central and eastern regions of the Pacific where larger skipjack tuna are common (Rothschild 1965; Doumenge[12]), but is similar to that in the western Indian Ocean (Marcille and Stequert 1976b). Again, gear selectivity in the different regions might account for this difference. However, skipjack tuna >65 cm FL appear to compose a portion (discarded) of the longline catch in the equatorial western Pacific (Wright footnote 11). Barkeley et al. (1978) concluded that skipjack tuna >4.5 kg (about 60 cm FL) would be unable to inhabit the warm surface water of the tropics, unless they were able to make frequent incursions into cooler water, for example below a shallow thermocline.

[10]Wańkowski, J. W. J., and D. W. Witcombe. 1979. Fish associated with floating debris in the equatorial western Pacific purse-seine fishery. Unpbul. manuscr., 13 p. Kanudi Fisheries Research Laboratory, P.O. Box 2417, Konedobu, Papua New Guinea.

[11]Wright, A., Fisheries Biologist, Kavieng Fisheries Research Laboratory, P.O. Box 101, Kavieng, Papua New Guinea, pers. commun. 1979.

[12]Doumenge, F. 1973. The development of tuna and skipjack fisheries in French Polynesia and experience in live-bait technique. South Pac. Comm. Fish. Newsl. 10:27-30.

Stock Movements

A stock is defined as the exploitable group of fish existing in a particular area at a particular time (Anonymous footnote 9). If it is assumed that a serial progression of length-frequency modes with time represents the progress of one group of fish through the fishery, then it should be possible to follow the movements of that group among the four fishing areas. While it is possible to do this, the analysis of skipjack tuna movements indicates only the complexity of the situation: groups of fish apparently moving freely and rapidly (often within 1 mo) between areas. No pattern nor periodic movement can be inferred from the present modal data. However, conclusions from Lewis (1980a, b, footnotes 3, 8) from the Papua New Guinea skipjack tuna tagging program are summarized below.

Skipjack tuna appear to be recruited from east of Papua New Guinea and from north of the Equator, and to move clockwise around the eastern and southern parts of the Bismarck Sea. Some fish appear to retrace this route up to 2 yr later, while others emigrate northward out of this area soon after recruitment. At least part of the stock, however, undergoes little translocation, remaining in one area for a considerable period of time. Most entries and exits appear to be through the northern Bismarck Sea between New Hanover and Manus. Some fish do not penetrate as far south as the eastern Bismarck Sea fishery, remaining in the New Hanover area only. While these results indicate extensive emigration and immigration, the skipjack tuna stocks cannot be considered purely transient since only a small portion of the tagged fish was recovered outside the Papua New Guinea region (although the variable distribution of fishing effort outside Papua New Guinea waters precludes definitive conclusions).

The present modal progressions indicate two types of movement of the yellowfin tuna: one commencing in the eastern Bismarck Sea, entering the area south of New Hanover and sometimes progressing to north of New Hanover (Figure 7, which shows those portions of the data in Figure 4, indicating movement of fish in the directions under discussion), and the reverse movement, indicated by the first appearance of a modal group to

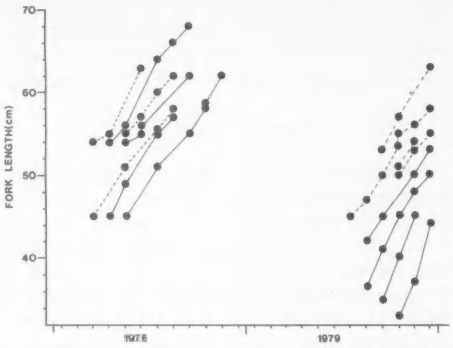

FIGURE 7.—Monthly modal progressions for yellowfin tuna in 1978 and 1979, showing apparent movement through the Papua New Guinea region from the eastern Bismarck Sea in a north and northwest direction through the New Hanover areas (line), and no apparent movement out of the area north of New Hanover (dashed line).

the north of New Hanover, or sometimes in the New Hanover area in general, and terminating in the eastern Bismarck Sea (Figure 8, which shows those portions of data in Figure 4, indicating the reverse movement of fish). A possible northward movement of yellowfin tuna recruited into the eastern Bismarck Sea in July and August 1977 is also indicated from the 1977 data (Figure 4).

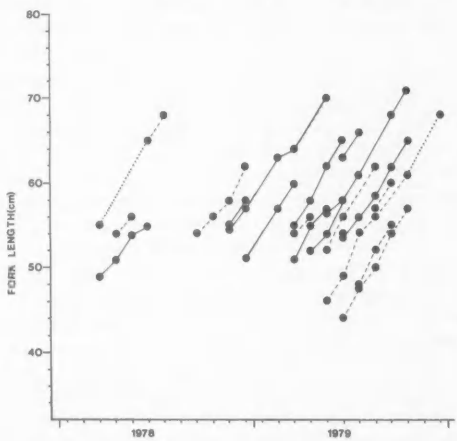

FIGURE 8.—Monthly modal progressions for yellowfin tuna in 1978 and 1979 showing apparent movement through the Papua New Guinea region from the New Hanover north area, south and southeast into the eastern Bismarck Sea area (line), and no apparent movement out of the Bismarck Sea (dashed line).

The periods of northward movement (of yellowfin tuna recruited to the eastern Bismarck Sea fishery in April and May 1978 and between August and October 1979) coincide with the appearance of small fish in the catch. However, since groups of fish of similar size appeared to move both north and south during 1978 and the first half of 1979, the direction of movement cannot be explained on the basis of size or age alone. During these periods of northward movement, all other groups of fish recruited to the fishery were restricted to the New Hanover area, almost exclusively to the north (Figure 4). These observations imply either a situation similar to that occurring in skipjack tuna where some fish penetrate no farther south than the New Hanover fishery or the northward movement of groups of fish that for some reason are not apparent in the Bismarck Sea catch. Groups of fish recruited at the same time as those moving in a southward direction (November 1978-June 1979) appeared to be restricted to the Bismarck Sea (Figure 4).

The results indicate extensive emigration and immigration of some of the yellowfin tuna stock, while other parts of the stock show little movement during their brief period of persistence in the fishery. The path taken appears similar to that shown by skipjack tuna stocks, and that proposed by Inoue (1969) for yellowfin tuna, not a surprising result in view of the geographical constraints of the region and the distribution of fishing effort. There is no evidence for emigration soon after recruitment, nor of source of recruitment, and groups of yellowfin tuna show mass movement either clockwise or anticlockwise through the Bismarck Sea with no indication of any retracing of their route.

Fundamental differences between the skipjack and yellowfin tuna stocks seem to lie in the long-term persistence of groups of skipjack tuna in the fishery (Figures 3, 4), probably an important function of their slower growth rate (Josse et al. 1979; present paper), while, in contrast, yellowfin tuna stocks remain in the exploitable size range for a few months only, since their faster growth rate (Le Guen and Sakagawa 1973; present paper) soon takes them out of the exploitable size range.

Estimated Length-At-Age

The von Bertalanffy parameters estimated from all data and all areas combined were $k = 0.0429$ and $L_\infty = 74.8$ cm for skipjack tuna, and $k = 0.0243$

and L_∞ = 180.9 cm for yellowfin tuna (k in both cases is estimated on a monthly basis). The calculated length-at-age curves are shown in Figures 9 and 10, which also include modal progression data fitted to the curve. Tables 2 and 3 list modal progressions used in the estimations. The mean square error was calculated from the formula:

$$\frac{\sqrt{\Sigma r^2}}{N}$$

where N is the number of pairs of observations and r a coefficient which is minimized in the curve fit.

$$r = \sqrt{\Sigma(\hat{L} - Li)^2}$$

where $\hat{L}$ is the length predicted by the particular curve and Li the observed length value. Since age at length data are unknown, r is not, strictly speaking, a true correlation coefficient. The mean square error was found to be 0.74 for the estimate of skipjack tuna growth and 2.01 for that of yellowfin tuna growth.

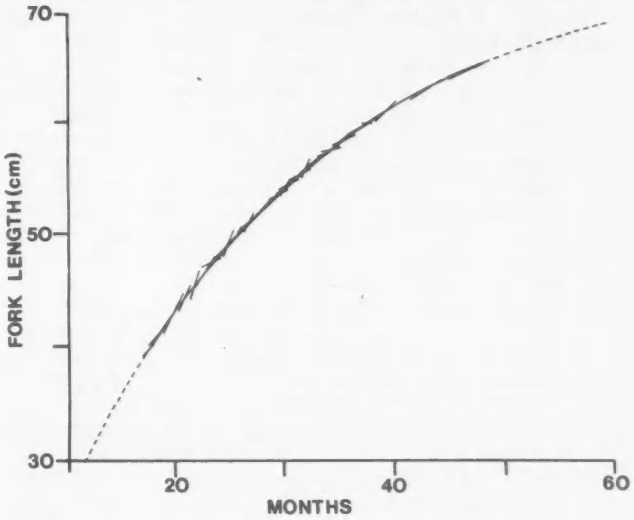

FIGURE 9.—Plot of length at age for skipjack tuna derived from all modal progressions for all Papua New Guinea areas combined, fitting the von Bertalanffy function by Fabens' (1965) procedure. Original modal data are shown fitted to the curve. The time scale is in elapsed months and does not indicate apparent age. Dashed line shows extrapolation beyond the range of observations.

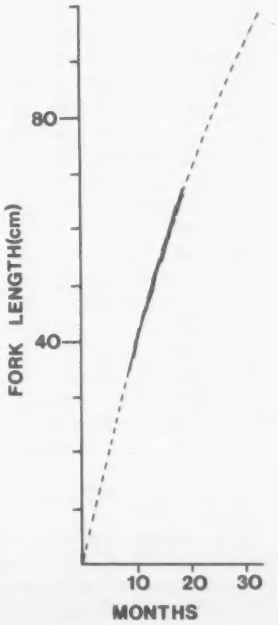

FIGURE 10.—Plot of length at age for yellowfin tuna derived from all modal progressions for all Papua New Guinea areas combined, fitting the von Bertalanffy function by Fabens' (1965) procedure. Original modal data are shown fitted to the curve. The time scale is in elapsed months and does not indicate apparent age. Dashed line shows extrapolation beyond the range of observations.

TABLE 2.—Modal progressions for skipjack tuna used to estimate fork length (centimers) at age. Modal progressions indicated by solid lines; $n = 83$.

Year	Month																							
1977	June		54																					
	July																							
	Aug.	57.5	55	51																				
	Sept.			52	51																			
	Oct.	58	56		52	51																		
	Nov.					52																		
1978	Mar.	58				48	47									38	39							
	Apr.	57	56		50											40	40							
	May	58	57			50	48									41								
	June		58	56	52	51	50.5																	
	July				53	52	51																	
	Aug.		59				52	50	50															
	Sept.			58	55			51	52	50														
	Oct.		60	59	56			52		51	50													
	Nov.			60	57	56		53			51													
	Dec.			60		57					52	50												
1979	Jan.											52												
	Feb.											53												
	Mar.				60							54					53							
	Apr.											55	54.5		50	49	44	43						
	May				62								55	54		50	47	45.5						
	June												57		52		48	47						
	July			65										56	53	52		48	45					
	Aug.				64		47	41	40				58		54	53.5	50	49						
	Sept.			66		52	48			42	39		59			55	51	50	48					
	Oct.				65			45	43	43	40			58			52		49					
	Nov.					54	50		44	44								52						
	Dec.					55					42													

TABLE 3.—Modal progressions for yellowfin tuna used to estimate fork length (centimeters) at age. Modal progressions indicated by solid lines; $n = 105$.

Year	Month																							
1977	July	63.5	56.5	51																				
	Aug.	58	58		51																			
	Sept.			59	54	50																		
	Oct.			64		54	61																	
	Nov.			68	61		65	50	46															
	Dec.				65	61		55	49															
1978	Jan.																							
	Feb.																							
	Mar.	54	49	45		70																		
	Apr.	55	51		54		45																	
	May		54	51	55		49	45	55															
	June	63	56						57	65														
	July		58	55.5	64		55	51	60	68														
	Aug.			58	68		57		62		55													
	Sept.		62		61			55			58	54												
	Oct.							58				56	58.5											
	Nov.											58	62	54.5	55									
	Dec.											62		57	58	51								
1979	Jan.																							
	Feb.													63		57								
	Mar.	55	54	51										64		60								
	Apr.	58	56	55	52																			
	May	62		57	54	46	48	52	56.5					70										
	June	65			58	49	50	56	58	44	47	53.5	63											
	July				61	54				46.5	51	56	66	45	48									
	Aug.					56		62		50	55	58.5		47	52	36.5	42	57						
	Sept.	53			68					54		62		50	55	41	45	60	35					
	Oct.	57	33	50	71	61	51			57		65		53.4		45			40					
	Nov.		37	53			54	43						56		48	50		45					
	Dec.		44	55		68		45		63				58		50	53							

DISCUSSION

The use of the von Bertalanffy function for estimating length-at-age implies that this function is a valid description of growth of skipjack and yellowfin tunas and that growth of all groups of each species is identical. Kearney (1978) has speculated that growth of skipjack tuna may be better represented by a number of linear stanzas, and an examination of the modal progression data indicates a disparity in growth rates among groups of fish. It should be noted that Knight

(1968), and others since, have pointed out the dangers of extrapolating the results beyond the range of observations on which they are based. However, provided that these limitations are recognized, and the results considered as representative of average growth of the stock, the length-at-age data are reasonable estimates of growth during the period of the study.

However, several qualifying comments must be made regarding these estimates. Length-frequency samples are subject to errors from two main sources: 1) Suzuki (1971) showed that samples obtained using a size-specific fishing technique are unlikely to be representative of the size class sampled. Fish at either extreme of the size range would be underrepresented: the mean length of modal groups is likely to be overestimated at the lower extreme and underestimated at the upper. 2) Josse et al. (1979) demonstrated that the modal progression method is sensitive to inadequate sampling: estimated growth rates vary widely if few landings are sampled. However, since daily landings from virtually every operating vessel were sampled, possible problems arising from the second source of error were minimized, if not eliminated entirely. The modal progression method itself is considered to be subjective (e.g., Joseph and Calkins 1969), both in view of the methods used to determine modal lengths and in connecting modal values to form serial progressions. However this technique has proved effective provided that the derived growth functions are considered estimates only.

Various studies on the growth of skipjack and yellowfin tunas have been conducted throughout the world, but few have been carried out in the western Pacific. Good estimates for the growth of medium-sized skipjack tuna are available from the Papua New Guinea tagging study. As Le Guen and Sakagawa (1973) pointed out, a comparison of the von Bertalanffy parameters k, L_∞, and t_0 often gives the misleading impression that growth is different in different regions. Two recent studies on yellowfin and skipjack tuna growth (Le Guen and Sakagawa 1973; Marcille and Stequert 1976b) compare these parameters from various regions and studies. In this paper, calculated growth curves from various studies in the Pacific Ocean are compared with those obtained by the present study. Such comparison requires the use of a common time base, in the form of apparent or estimated age, which may be achieved by fixing one common age at length for each species. In the absence of a reliable method for aging skipjack or yellowfin tuna it is necessary to estimate likely age at length by combining results obtained using several techniques.

Estimates of fork length of skipjack tuna at age 12 mo agree very closely. Batts (1972) and Cayre[13] used dorsal spine readings to obtain lengths of 40.6 and 40.7 cm for the western and eastern Atlantic. Yoshida (1971), using modal progression data from juveniles recovered from the stomachs of billfish, and Uchiyama and Struhsaker[14] from readings of sagittae, estimated lengths of 35.0 and 42.6 cm for the central Pacific. Finally Lewis (footnote 3), also reported in Josse et al. 1979) reported estimates from Papua New Guinea waters of between 40.0 and 45.0 cm, again from sagittal readings. In the present study an approximate average of these quoted figures was used: 40.0 cm at 12-mo age.

In comparing growth curves for skipjack tuna from different regions, only those from the Pacific have been used (Figure 11), since Josse et al. (1979) showed that, due to sample variability, no significant difference was detectable in growth among regions, nor between growth in the eastern and western Pacific as calculated from tagging studies. Underestimation (Josse et al. 1979) of growth of larger fish and their low L_∞ (65.47 cm) may account for the difference in slope of the two curves derived for Papua New Guinea skipjack tuna, and for the difference in the two values of k (Josse et al. 1979: $k = 0.9451$; present paper: $k = 0.5148$, both estimated on an annual basis).

Age at length estimates for yellowfin tuna obtained from scale readings and modal progression data show good agreement over the range of observed values only (Suzuki 1971; Le Guen and Sakagawa 1973), with the exception of the study by Yabuta et al. (1960) which appears to have underestimated growth rate. Estimates for age at length have been obtained for yellowfin tuna from the Atlantic from scale readings by Yang et al. (1969), whose observed fork lengths averaged 66.1 cm at 18-mo age, and by calculation from spawning and recruitment data (Le Guen et al. 1969). The latter study estimated fork length at 18 mo to

[13]Cayre, P. 1978. Determination de l'age de listao *Katsuwonus pelamis* L., debarques a Dakar. Int. Comm. Conserv. Atl. Tuna, Collect. Sci. Pap., SCR 78/50.

[14]Uchiyama, J. H., and P. Struhsaker. 1975. Age and growth of skipjack tuna, *Katsuwonus pelamis*, yellowfin tuna, *Thunnus albacares*, and albacore, *Thunnus alalunga*, as indicated by daily growth increments of sagittae. Int. Comm. Conserv. Atl. Tuna, SCRS 75/57.

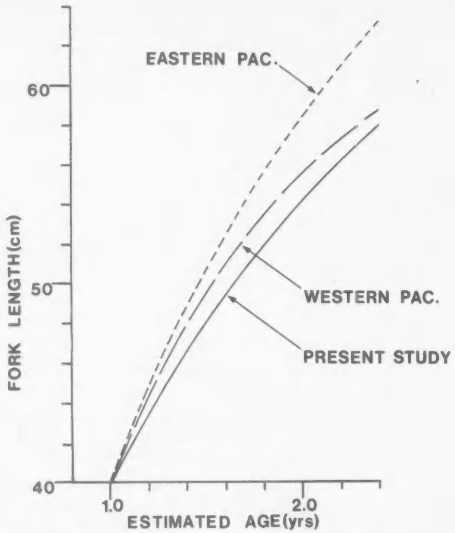

FIGURE 11.—Comparison of growth curves for skipjack tuna from the Pacific. Growth in the eastern Pacific (dashed line) was recalculated from various tagging studies by Josse et al. (1979); in the western Pacific from tagging (Josse et al. 1979, broken line) and modal progressions (present study, line). All are adjusted to a common base age of 12 mo at 40.0 cm FL. Data from Josse et al. (1979) were calculated by them using Tomlinson's (1971) least squares procedure.

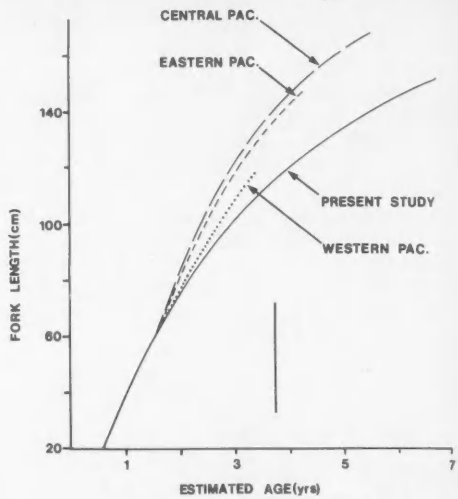

FIGURE 12.—Comparison of growth curves for yellowfin tuna from the Pacific. Eastern Pacific (Davidoff 1963, dashed line); central Pacific (Moore 1951, broken line); western Pacific (Yabuta et al. 1960, dotted line); and present study (line). All were recalculated using Fabens' (1965) least squares procedure. Vertical bar indicates limits of data used to derive the present curve; extrapolation beyond this range is for comparison purposes only.

be 60.0 cm, the value used in the present comparison.

Growth estimates of yellowfin tuna from the eastern Pacific (Davidoff 1963), central Pacific (Moore 1951), and western Pacific (Yabuta et al. 1960) were recalculated by Le Guen and Sakagawa (1973) using Fabens' (1965) method and are compared with the results of the present study (Figure 12). The recalculated lengths-at-age were in all cases similar to those obtained by the original authors. Although the above studies were carried out on large fish within the 47-170 cm FL range, their L_∞ values were only slightly higher (188.4-200.3 cm) than that obtained in the present study. The major difference lies in rate of growth, and, although extrapolation of the present results beyond 71 cm is dangerous, these results and those of Yabuta et al. (1960) imply that growth of yellowfin tuna in the western Pacific may be substantially slower than in the central and eastern Pacific. Marcille and Stequert (1976a) studied growth of pole-and-line caught yellowfin tuna of a similar length range (45-75 cm FL) in the equatorial western Indian Ocean. Their reported growth rate of 17-19 cm/6 mo for this size range of fish is similar to the results of the present study. A further possible explanation for this apparent disparity between growth in large and small yellowfin tuna may be simply that the von Bertalanffy function does not adequately describe yellowfin tuna growth, and that yellowfin tuna may undergo changes in growth pattern, due to movement into deeper water, for example.

A point of ecological importance is the great difference in growth rate between skipjack and yellowfin tunas of the same size. Yellowfin tuna grow to over 180 cm FL, over twice the length of skipjack tuna and almost 20 times the body weight. Studies on skipjack and yellowfin tunas' bioenergetics (Kitchell et al. 1978), although indicating a qualitative similarity between the two species, demonstrated that the metabolic rate of adult skipjack tuna, unlike that of yellowfin tuna and most other fishes, is independent of body weight. This may reflect the apparently less efficient hydrodynamics of skipjack tuna, a conse-

quence of the absence of a swim bladder and relatively small surface area of the pectoral fins, in comparison with yellowfin tuna.

Although over half of the tuna schools in Papua New Guinea waters are pure skipjack tuna (West and Wilson[15]), about 40% contain a mixture of yellowfin and skipjack tunas, and only about 5% are pure yellowfin tuna. Length-frequency sampling has demonstrated that yellowfin and skipjack tunas taken from any single mixed school comprise a similar size range, although observations indicate that larger yellowfin tuna (estimated to be in the 70-130 cm size range) are frequently present. Since yellowfin tuna grow so much faster than skipjack tuna, the yellowfin tuna members of a mixed school must, within a matter of a few weeks, outgrow their skipjack tuna counterparts. Such a situation would lead either to the break-up of the school as a consequence of divergence in size, or persistence of large-size yellowfin tuna in a school comprising mainly smaller skipjack tuna. Observations have indicated that the latter situation occurs during certain periods.

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LITERATURE CITED

BARKLEY, R. A., W. H. NEILL, AND R. M. GOODING.
1978. Skipjack tuna, *Katsuwonus pelamis*, habitat based on temperature and oxygen requirements. Fish. Bull., U.S. 76:653-662.

BATTS, B. S.
1972. Age and growth of the skipjack tuna, *Katsuwonus pelamis* (Linnaeus), in North Carolina waters. Chesapeake Sci. 13:237-244.

BERTALANFFY, L. VON.
1960. Principles and theory of growth. *In* W. W. Nowinski (editor), Fundamental aspects of normal and malignant growth, p. 137-259. Elsevier, Amst.

BOUR, W., AND P. GALENON.
1979. The development of tuna fisheries in the western Pacific. South Pac. Comm., Noumea, New Caledonia, Occas. Pap. 12, 34 p.

DAGET, J., AND J. C. LE GUEN.
1975. Les critères d'age chez les poissons. *In* M. Lamotte and F. Bourlière (editors), Problèmes d'écologie, p. 253-289. Masson et Cie, Paris.

DAVIDOFF, E. B.
1963. Size and year class composition of catch, age and growth of yellowfin tuna in the Eastern Tropical Pacific Ocean, 1951-1961. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 8:199-251.

FABENS, A. J.
1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29:265-289.

HENNEMUTH, R. C.
1961. Size and year class composition of catch, age and growth of yellowfin tuna in the eastern tropical Pacific Ocean for the years 1954-1958. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 5:1-112.

INOUE, M.
1969. Perspective on exploitation of fishing grounds for skipjack and young yellowfin tuna in the western tropical Pacific. Bull. Jpn. Soc. Fish. Oceanogr. Spec. No. Professor Uda's Commemorative Papers, p. 235-241.

JOSEPH, J., AND T. P. CALKINS.
1969. Population dynamics of the skipjack tuna (*Katsuwonus pelamis*) of the eastern Pacific Ocean. [In Engl. and Span.] Inter-Am. Trop. Tuna Comm., Bull. 13:1-273.

JOSSE, E., J. C. LE GUEN, R. E. KEARNEY, A. D. LEWIS, A. SMITH, L. MAREC, AND P. K. TOMLINSON.
1979. Growth of skipjack. South Pac. Comm., Noumea, New Caledonia, Occas. Pap. 11, 83 p.

KEARNEY, R. E.
1978. Some hypotheses on skipjack (*Katsuwonus pelamis*) in the Pacific Ocean. South Pac. Comm., Noumea, New Caledonia, Occas. Pap. 7, 34 p.

KIKAWA, S., AND I. WARASHINA.
1972. The catch of the young yellowfin tuna by the skipjack pole-and-line fishery in the southern area of the western Pacific Ocean. [In Jpn., Engl. summ.] Bull. Far Seas Fish. Res. Lab. (Shimizu) 6:39-49.

KITCHELL, J. F., W. H. NEILL, A. E. DIZON, AND J. J. MAGNUSON.
1978. Bioenergetic spectra of skipjack and yellowfin tunas. *In* G. D. Sharp and A. E. Dizon (editors), The physiological ecology of tunas, p. 357-368, Acad. Press, N.Y.

KNIGHT, W.
1968. Asymptotic growth: an example of nonsense disguised as mathematics. J. Fish. Res. Board Can. 25:1303-1307.

LE GUEN, J. C., F. BAUDIN-LAURENCIN, AND C. CHAMPAGNAT.
1969. Croissance de l'albacore (*Thunnus albacares*) dans les régions de Pointe-Noire et de Dakar. Cah. O.R.S.T.O.M., sér. Océanogr. 7:19-40.

[15]West, G. J., and M. A. Wilson. An aerial survey of the tuna resources of Papua New Guinea. Unpubl. manuscr. Kanudi Fisheries Research Laboratory, P.O. Box 2417, Konedobu, Papua New Guinea.

LE GUEN, J. C., AND G. T. SAKAGAWA.
1973. Apparent growth of yellowfin tuna from the eastern Atlantic Ocean. Fish. Bull., U.S. 71:175-187.

LEWIS, A. D.
1980a. Tagging of skipjack tuna (*Katsuwonus pelamis*) in Papua New Guinea waters, 1971-1972. Dep. Primary Ind., Port Moresby, Papua New Guinea, Res. Bull. 25, 25 p.
1980b. Tagging of skipjack tuna (*Katsuwonus pelamis*) in Papua New Guinea waters, 1973-1974. Dep. Primary Ind., Port Moresby, Papua New Guinea, Res. Bull. 26, 34 p.

MARCILLE, J., AND B. STEQUERT.
1976a. Croissance du jeunes albacores, *Thunnus albacares*, et patudos, *Thunnus obesus*, dans la côte nord-oust de Madagascar. Cah. O.R.S.T.O.M., sér Océanogr. 14:153-162.
1976b. Etude préliminaire de la croissance du listao (*Katsuwonus pelamis*) dans l'ouest de l'Océan Indien tropical. Cah. O.R.S.T.O.M., sér Océanogr. 14:139-151.

MATSUMOTO, W. M.
1966. Distribution and abundance of tuna larvae in the Pacific Ocean. *In* T. A. Manar (editor), Proceedings of the Governor's Conference on Central Pacific Fishery Resources, State of Hawaii, p. 221-230.

MOORE, H. L.
1951. Estimation of age and growth of yellowfin tuna (*Neothunnus macropterus*) in Hawaiian waters by size frequencies. U.S. Fish Wildl. Serv., Fish. Bull. 52:133-149.

NAGANUMA, A.
1979. On spawning activities of skipjack tuna in the western Pacific Ocean. Bull. Tohoku Reg. Fish. Res. Lab. 40:1-13.

NISHIKAWA, Y., S. KIKAWA, M. HONMA, AND S. UEYANAGI.
1978. Distribution atlas of larval tunas, billfishes, and related species–Results of larval surveys by R.V. *Shunyo Maru* and *Shoyo Maru* (1956-1975). [In Jpn., Engl. summ.] Far Seas Fish. Res. Lab. (Shimizu), S Ser., 9, 99 p.

RICHARDS, W. J.
1969. Distribution and relative apparent abundance of larval tunas collected in the tropical Atlantic during Equalant surveys I and II. *In* Abidjan 1966, p. 289-315. Proc. Symp. Oceanogr. Fish. Resour. Trop. Atl., UNESCO, Paris.

ROTHSCHILD, B. J.
1965. Hypotheses on the origin of exploited skipjack tuna (*Katsuwonus pelamis*) in the eastern and central Pacific Ocean. U.S. Fish Wild. Serv., Spec. Sci. Rep. Fish. 512, 20 p.
1967. Estimates of the growth of skipjack tuna (*Katsuwonus pelamis*) in the Hawaiian Islands. Indo-Pac. Fish. Counc., Proc. 12th Sess., Sect. 2:100-111.

SCHAEFER, M. B., AND R. J. H. BEVERTON.
1963. Fishery dynamics—their analysis and interpretation. *In* M. N. Hill (editor), The Sea, Vol. 2, p. 464-483. Wiley, N.Y.

SUZUKI, Z.
1971. Comparison of growth parameters estimated for the yellowfin tuna in the Pacific Ocean. Bull. Far Seas Fish. Res. Lab. (Shimizu) 5:89-105.

TOMIYAMA, T., AND T. HIBIYA.
1976. Fisheries in Japan *Skipjack* and *mackerel*. Japan Marine Products Photo Materials Association, Tokyo, 162 p.

TOMLINSON, P. K. (programmer).
1971. Program name–BGC 4. *In* N. J. Abramson (compiler), Computer program for fish stock assessment, p. 2.(5).3.1 to 2.(5).3.3. FAO Fish. Tech. Pap. 101.

UEYANAGI, S.
1970. Distribution and relative abundance of larval skipjack tuna (*Katsuwonus pelamis*) in the western Pacific Ocean. *In* J. C. Marr (editor), The Kuroshio: a symposium on the Japan current, p. 395-398. East-West Center Press, Honolulu.

WANKOWSKI, J. W. J.
1980. Recent history and summarized statistics of the industrial fisheries for tuna and tuna-like species in the area of the Papua New Guinea Declared Fisheries Zone, 1970-1979. Dep. Primary Ind., Port Moresby, Papua New Guinea, Res. Bull. 24, 82 p.

WRIGHT, A.
1980. An investigation of Japanese longline tuna fishing operations in the western equatorial Pacific. Dep. Primary Ind., Port Moresby, Papua New Guinea, Res. Bull. 23, 44 p.

YABUTA, Y., M. YUKINAWA, AND Y. WARASHINA.
1960. Growth and age of yellowfin tuna. II. Age determination (scale method). Rep. Nankai Reg. Fish. Res. Lab. 12:63-74.

YANG, R. T., Y. NOSE, AND Y. HIYAMA.
1969. A comparative study on the age and growth of yellowfin tunas from the Pacific and Atlantic Oceans. Bull. Far Seas Fish. Res. Lab. (Shimizu) 2:1-21.

YOSHIDA, H. O.
1971. The early life history of skipjack tuna, *Katsuwonus pelamis*, in the Pacific Ocean. Fish. Bull., U.S. 69:545-554.

GROWTH, REPRODUCTION, AND FOOD HABITS OF OLIVE ROCKFISH, *SEBASTES SERRANOIDES*, OFF CENTRAL CALIFORNIA

MILTON S. LOVE AND WILLIAM V. WESTPHAL[1]

ABSTRACT

We collected data on age-length and length-weight relationships, age at first maturity, spawning season, fecundity, and food habits of olive rockfish, *Sebastes serranoides*, off Diablo Cove, near Avila, California. Fish were aged from otoliths. Von Bertalanffy age-length parameters for females were $L_\infty = 51.9$, $k = 0.18$, and $t_0 = -1.57$; for males $L_\infty = 43.3$, $k = 0.27$, and $t_0 = -1.03$. Females grew at a faster rate than males beginning at the age where most males were mature. Age at first maturity ranged from 3 to 8 years, most fishes maturing by age 6. Olive rockfish spawned once per season, between December and March, with peak spawning in January. Fecundity ranged between 30,000 and 490,000 eggs. Small individuals preyed primarily on plankton, and larger ones concentrated on fishes, squids, and octopuses.

The rockfishes (Scorpaenidae: *Sebastes*) are an important constituent of many marine communities in the eastern North Pacific. Sixty-nine species are known to inhabit these waters (Lea and Fitch 1979) and members of the genus frequent virtually every habitat from intertidal regions to depths of well over 1,000 m.

Though these fishes were of some importance in commercial and sport fisheries in the past, population declines of more popular fishes have led to a steady increase in rockfish demand. Commercial rockfish catches in the Northeast Pacific exceeded 30,000 t in 1978 (Pacific Marine Fisheries Commission 1980) and in California, rockfishes are the most important sport fishes, by number, in party boat catches (Pinkas 1977).

Major, deeper water, commercially important species, such as Pacific ocean perch, *S. alutus* (Westrheim 1973; Gunderson 1977; Wishard et al. 1980); chilipepper, *S. goodei*, and bocaccio, *S. paucispinis* (Phillips 1964; Wilkins 1980; Wishard et al. 1980); and yellowtail rockfish, *S. flavidus* (Phillips 1964; Carlson and Haight 1972; Wishard et al. 1980) have received most attention from researchers. By contrast, with the exception of blue rockfish, *S. mystinus* (summarized in Miller and Geibel 1973), there are few papers on inshore rockfishes.

The olive rockfish, *Sebastes serranoides*, composes a major portion of the sport fish catch, both from party boats and private vessels, along southern and central California (Miller and Gotshall 1965; Wine and Hoban[2]; Maxwell and Schultze[3]). It lives in areas of reef and kelp, from Del Norte County, Calif., to San Benito Island, Baja California, Mexico, and is most abundant in depths of 5-100 m.

Olive rockfish are active, fast-swimming, streamlined predators, usually found in the water column, but occasionally hovering over or resting upon rocky substrates (Quast 1968a; Hobson and Chess 1976; Love and Ebeling 1978). Juvenile olive rockfish are primarily midwater feeders, preying upon zooplankton and small fishes, though some substrate feeding (on isopods, caprellid amphipods, etc.) has been noted (Quast 1968b; Hobson and Chess 1976; Love and Ebeling 1978). No data were available on the food habits of adults. Once they settle out of the plankton, individuals apparently grow to adulthood in a relatively small, circumscribed area (Love 1980) and reefs can be readily depleted of large individuals by overfishing. Off Santa Barbara, Calif., the diminishing sport catch of olive rockfish is now mostly of juvenile and subadult fish, younger than the age of first maturity (Love 1980). Yet, despite

[1]Department of Biology, Occidental College, 1600 Campus Road, Los Angeles, CA 90041.

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[2]Wine, V., and T. Hoban. 1976. Southern California independent sportfishing survey annual report July 1, 1975-June 30, 1976. Calif. Dep. Fish Game, 109 p.

[3]Maxwell, W. D., and D. L. Schultze. 1976. Southern California partyboat sampling study. Calif. Dep. Fish Game, Mar. Res. Adm. Rep. No. 76-3, 18 p.; 76-6, 18 p.; 76-9, 13 p.

the importance and vulnerability of the olive rockfish, little was known about its life history.

METHODS

Specimens were collected between 1972 and 1977, at a group of shallow-water pinnacles, about 11 km west of Avila, Calif. (Figure 1). These pinnacles, at depths of 20-30 m, are situated 100-300 m offshore from Diablo Cove and North Cove, and rise to within 5-10 m of the surface. Brown algae (predominantly *Nereocyctis* sp.) grow on the shallower reefs during summer and fall. Sampling was sporadic until 1975, when, with a few exceptions, monthly collections were made through 1977.

Specimens were collected by hook and line and by pole spear (in about equal proportions), immediately placed on ice aboard the diving vessel, and then frozen for later examination ashore.

All specimens were measured (total and standard lengths—TL, SL) to the nearest millimeter and weighed to the nearest 0.1 g. Individuals larger than about 15 cm TL were sexed and their gonads weighed to the nearest 0.1 g.

Age Determination

Attempts to age rockfish have utilized various calcified structures (scales: Phillips 1964; Miller and Geibel 1973; otoliths: Chen 1971; Patten 1973; Westrheim and Harling[4]; vertebrae, opercles, otoliths, scales, anal pterygiophores, etc.: Six and Horton 1977), each with varying success. Otoliths and scales have been most useful, and in this study fish were aged with saccular otoliths. Sagittae were removed from 616 (320 female and 296 male) specimens. Otoliths were cleaned and stored in water. Often thick and difficult to read, otoliths from *S. serranoides* older than about 7 yr were immersed in clove oil for several months to increase their transparency. A chalky coating covering an occasional otolith was cleared away with a weak hydrochloric acid solution. Care was taken to prevent dissolving annuli at the otolith margins.

Otoliths were placed in a black-bottomed watchglass filled with water (or clove oil) and read under a dissecting microscope at a magnification of 10×. All otoliths were read twice, by the senior author, approximately 2 mo apart. Agreement between reading was highest (100%) in 0-yr fish, declining to 25% in 14-yr-olds (Table 1). If the readings did not agree, the otoliths were read again. The value of two coincident readings was accepted as the best estimate of age. If all three readings were different, the midreading was accepted. A few otoliths were rejected as unreadable due to fluctuations in readings of as much as 4 yr.

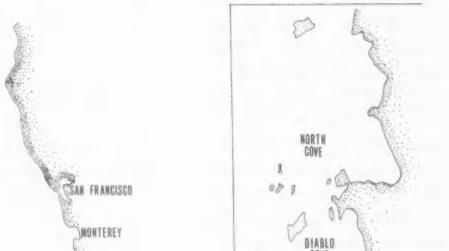

FIGURE 1.—Location of sampling sites (marked with an x) for olive rockfish off Diablo Cove, Calif.

TABLE 1.—Consistency (percent agreement) of duplicate readings from olive rockfish. The readings were made 2 mo apart by the same observer.

No. of zones	Otoliths (no.)	Percent	No. of zones	Otoliths (no.)	Percent
0	45	100	8	60	72
1	12	100	9	45	69
2	55	98	10	37	63
3	72	94	11	15	58
4	66	83	12	10	40
5	72	83	13	8	38
6	74	80	14	12	25
7	73	77			

Maturation and Reproduction

The gonads of mature olive rockfish undergo marked, yearly cyclical changes. Immediately after larvae are released spent ovaries are flaccid and reddish, purple, or gray. A resting period follows as the ovaries firm up, turning pink-red. Ovaries turn bright orange (very rarely cream-colored) and contain opaque eggs, during the mature phase, before fertilization. During the

[4]Westrheim, S. J., and W. R. Harling. 1975. Age-length relationships for 26 scorpaenids in the northeast Pacific Ocean. Can. Fish. Mar. Serv., Res. Dev., Tech. Rep 565, 12 p.

fertilized stage, the eggs are clear and turn gray as larvae develop in the ripe ovaries.

Mature males undergo a simpler cycle. Resting stage testes are small and brown, becoming larger and whitish brown as they develop. Fully developed testes are large, white, and delicate.

With this information, it was possible to determine when fish reproduced and when insemination occurred. Stages of gonad maturation (condition) in 1,056 adult olive rockfish, taken during 1972-77, were determined using the criteria of Westrheim (1975). A gonadosomatic index (gonad weight)/(total body weight) × 100 was computed to quantify changes in gonad size with season.

For fecundity estimates the ovaries of 83 mature fish captured in October and November were placed in modified Gilson's solution (100 ml 60% isopropanol, 880 ml freshwater, 15 ml 80% nitric acid, 18 ml glacial acetic acid, and 20 g mercuric chloride—Bagenal and Braum 1971) to harden the eggs and were periodically shaken to loosen them from ovarian tissue. Eggs were kept in the solution for about 2 mo, after which the fluid was poured off and replaced with water. Before eggs were counted, the ovaries were further broken up and repeatedly washed with water to remove remaining connective tissue. The eggs were placed in a larger beaker and water was then added until 2,000 ml of eggs and water had been obtained. The mixture was stirred magnetically until the eggs were homogeneously distributed throughout the water column, and a 5 ml subsample was drawn with a pipette. Three subsamples were taken.

Eggs in each subsample were counted, using a dissecting microscope, and the mean number per milliliter was calculated for the three subsamples. Fecundity was then estimated by back calculation.

Food Habits

Specimens were collected nearly every month between May 1975 and April 1977 by hook and line and pole spear (in about equal proportions), immediately placed on ice aboard the diving vessel, and frozen soon after for later examination ashore. A total of 591 specimens were collected, of which 374 (63.3%) had some food in their stomachs. We took precautions that only artificial lures were used and chumming or other disturbances were avoided, so that sampling method did not bias the stomach content composition.

Stomach contents were sorted taxonomically into 17 food items and the volume of each category was measured by liquid displacement. Food items were also grouped into three prey types (substrate oriented, nekton, and plankton) based on prey behavior and habitat. Nektonic prey included all nonlarval fish and squid. Substrate-oriented prey included all prey (except fish) that live on or about reef and plant surfaces; these may be motile, such as octopus, or attached, like algae.

To examine seasonal variation in diet within each size class of olive rockfish (except 10.1-20.0 cm which had too few specimens), food data was pooled by seasonal periods roughly corresponding to "upwelling" (March-August) and "oceanic" (September-February) oceanographic regimes off the Avila area (Bakun 1973).

RESULTS AND DISCUSSION

Age and Growth

There was no published work in aging olive rockfish (with the exception of a few fish mentioned in Burge and Schultz[5]), and the use of the otoliths in age studies had not been validated. To determine if the opaque and translucent zones were annular, we observed the development of the opaque zone on the edge of otoliths of fish from Avila, taken during a 5-yr period. The occurrence of a particular zone among most or all individuals during one part of the year would indicate that the zones were suitable for age determination (Williams and Bedford 1974; Dark 1975). Because the opaque zones become narrow and difficult to distinguish in older fish and the timing of zone deposition may be influenced by the species' age or state of maturity (Williams and Bedford 1974; Dark 1975), we limited sampling for otolith validity to 1- to 3-yr-old (immature) olive rockfish.

Data indicated that the opaque zone deposition was seasonal (Figure 2). The percentage of otoliths with opaque edges was low during fall and winter, but rose abruptly during late spring and peaked in summer months. Hence, the production of opaque zones coincides with the upwelling period along central California (Bakun 1973) and probably reflects increased feeding and growth. The percentage of opaque zones during the early spring may be underestimated as the newly deposited opaque material is quite thin. On the other hand,

[5]Burge, R. T., and S. A. Schultz. 1973. The marine environment in the vicinity of Diablo Cove with special reference to abalones and bony fishes. Calif. Dep. Fish Game, Mar. Res. Tech. Rep. 19, 433 p.

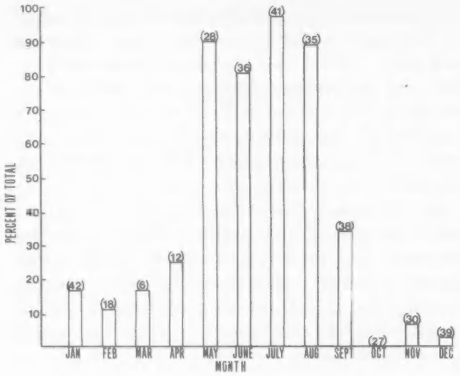

FIGURE 2.—Monthly percentages of 1- to 3-yr-old olive rockfish with opaque margins. Sample size is in parentheses.

the beginnings of the transparent zone during the fall are readily apparent.

Lengths at ages were estimated by direct observation of otolith annuli, back calculation of annuli, and through the von Bertalanffy growth curve model. In this model, the formula

$$L_t = L_\infty [1 - \exp -k(t - t_0)]$$

where L_t = length at time t
L_∞ = theoretical maximum length
k = constant expressing the rate of approach to L_∞
t_0 = theoretical age at which $L_t = 0$

was fitted to the direct observation age-length data.

We transformed the male and female von Bertalanffy growth equations to linear form (Allen 1976) and compared these by analysis of variance. Females were found to grow significantly faster than males ($F = 19.08$, $P < 0.01$), hence we have separated growth data by sex (Table 2).

Mean lengths at ages obtained by direct observations of annuli and as generated by the von Bertalanffy equations are plotted to age 14 (Figure 3). Through direct observation of annuli, we found

TABLE 2.—Parameters of the von Bertalanffy equation for olive rockfish off Diablo Canyon, Calif.

Sex	L_∞	SE	k	SE	t_0	SE
Females	51.90	0.93	0.18	0.01	−1.57	0.23
Males	43.30	.45	.27	.02	−1.03	.19

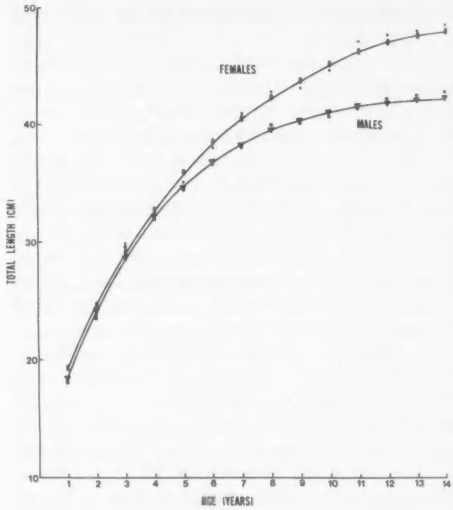

FIGURE 3.—Von Bertalanffy growth curves of female (circles) and male (triangles) olive rockfish. Also included are mean lengths at ages (females—stars, males—dots) computed from direct observation of otolith annuli. Based on 320 females and 296 males taken off Diablo Cove, 1972-77.

a few individuals to live to be as much as 25 yr. However, our samples of fishes older than about 14 yr were few, and older fish played little part in growth calculations. Back-calculated lengths (Tables 3, 4) were computed to age 12. Otoliths of fish older than 12 yr were often unusable for back calculations, because these fish laid down heavy layers of opaque material along the axis used to measure annuli, making measurements difficult.

All three measures of growth yielded similar results. Mean lengths at age for females and males were similar through age 4. Females outgrew males beginning at age 5, the age at which over 50% of the males were mature. Both male and female olive rockfish had k values (0.27 and 0.18, respectively) higher than most previously studied rockfish, indicating that the species reached maximum length relatively quickly. The k-values were similar (though slightly higher for both sexes) to those of *S. flavidus* (Fraidenburg 1980; Westrheim and Harling footnote 4), a closely related species.

Because few individuals older than 14 yr were captured, estimates of length at age of older fish produced by the von Bertalanffy equation may be inaccurate. Certainly the L_∞'s are too low, as

TABLE 3.—Mean back-calculated total length (centimeters) ± 95% confidence intervals at successive annuli for male olive rockfish captured off Avila during 1972-77.

Age-group	No. of fish	1	2	3	4	5	6	7	8	9	10	11	12
1	3	17.9±5.8											
2	24	18.5±1.0	22.8±0.6										
3	40	19.4±0.4	24.8±0.6	29.7±0.6									
4	34	18.7±0.6	24.9±0.8	29.5±0.6	33.0±0.6								
5	38	19.2±0.2	24.7±0.6	29.6±0.4	33.2±0.4	35.8±0.8							
6	33	19.1±0.8	24.2±0.8	29.0±0.8	32.7±0.6	35.0±0.6	36.7±0.6						
7	33	19.2±0.4	24.7±0.4	30.0±0.4	33.1±0.6	35.4±0.4	36.9±0.4	38.0±0.4					
8	27	18.7±0.6	24.1±0.6	30.4±0.8	33.4±0.6	36.0±0.6	37.2±0.6	38.3±0.6	39.4±0.6				
9	22	18.3±0.6	24.6±0.6	29.6±0.5	32.5±0.6	35.1±0.6	37.0±0.5	38.2±0.5	39.7±0.6	40.4±0.7			
10	14	17.8±0.1	22.8±0.3	28.6±1.2	32.4±1.0	35.9±1.0	36.3±1.2	38.1±0.4	38.0±1.1	39.4±1.1	41.1±1.3		
11	5	17.5±1.4	22.4±1.8	28.2±1.8	32.0±1.5	34.1±1.8	36.1±1.7	37.1±1.9	38.1±1.8	40.2±2.0	39.4±1.9	41.0±1.7	
12	9	18.1±1.5	22.5±1.4	29.0±1.3	32.6±1.7	35.0±1.5	36.5±1.4	37.4±1.4	38.5±0.5	39.3±1.5	41.4±1.5	40.8±1.4	40.9±1.6
Average		18.5	23.8	29.4	32.8	35.3	36.8	37.9	39.0	39.9	40.9	40.9	40.9

TABLE 4.—Mean back-calculated total length (centimeters) ± 95% confidence intervals at successive annuli for female olive rockfish captured off Avila during 1972-77.

Age-group	No. of fish	1	2	3	4	5	6	7	8	9	10	11	12
1	7	19.2±2.3											
2	24	18.1±0.8	24.0±0.8										
3	32	19.0±0.6	24.5±0.6	30.0±0.8									
4	31	19.4±0.6	24.9±0.8	29.8±0.8	33.7±0.8								
5	39	19.7±0.8	24.8±0.8	30.1±0.8	33.6±0.8	36.0±1.0							
6	35	19.1±0.6	24.4±0.8	28.7±1.0	32.6±1.0	35.2±1.0	37.9±1.0						
7	39	20.5±0.6	26.0±0.8	30.6±0.8	34.1±1.0	36.6±1.1	38.4±0.8	40.7±0.8					
8	32	19.6±0.1	24.8±0.3	31.0±0.5	35.1±0.3	37.1±0.3	39.3±0.4	41.9±0.5	42.6±0.2				
9	23	18.3±0.6	24.5±0.4	30.4±1.0	33.7±0.8	36.2±0.8	38.7±0.8	40.7±0.8	42.8±0.8	42.9±0.8			
10	23	20.3±0.2	26.3±1.3	31.0±1.3	34.6±0.9	36.1±1.3	38.1±1.1	40.1±1.2	41.7±1.4	42.8±1.2	43.9±1.1		
11	10	18.2±1.2	23.7±1.3	28.6±1.4	33.0±1.4	36.1±1.2	38.1±1.6	40.1±1.7	42.1±1.6	41.9±1.6	43.1±1.8	45.2±1.8	
12	4	18.2±1.4	24.0±1.6	28.3±1.8	33.3±1.6	35.4±1.9	38.3±2.0	40.3±2.1	41.9±1.6	41.6±2.1	42.9±1.6	45.1±1.8	45.6±1.9
Average		19.2	24.8	29.9	33.7	36.2	38.5	40.7	42.2	42.4	43.5	45.2	45.6

we did capture females to 61.9 cm and males to 50.2 cm.

No marked Lee's Phenomenon was noted, though it is found in other rockfishes (Chen 1971; Miller and Geibel 1973). A possible explanation is that fish older than age 12 were not used in back calculations, and since some members of the species live to at least 25 yr, the phenomenon may not be apparent until older fish are examined.

Length-Weight Relationships

A total of 312 males and 304 females were weighed and measured. The relationships between total length and weight seemed to fit the relationships $W = aL^b$, where W = weight in grams and L = total length in centimeters, and a and b are constants. The values of a and b were determined using $\log_{10}$ transformation and fitting the values to a straight line by least squares. Females tended to be heavier at a given length (analysis of variance, $F = 15.23$, $P < 0.01$) (Figures 4, 5). To test whether this difference was an artifact caused by the larger female gonads, we subtracted gonad weight from body weight, generated the length-weight relationships for each sex and tested these between sexes. Again, females were heavier at length (analysis of variance, $F = 10.18$, $P < 0.01$).

Maturation and Reproduction

Insemination and Birthing Season

Larval release occurred from December through March, peaking during January (Figure 6). Spent females were most prevalent during early spring, followed by a June peak in resting fish and a September-October peak in mature individuals. Fertilized fish were found from November through January. Ovary weights remained essentially constant during the spring and summer (Figure 7), averaging perhaps 0.3% of body weight, occasionally as little as 0.1%. Then, during the winter and spawning season, ripe ovaries averaged 13.8% of body weight (maximum 20.7%, minimum 2.3%).

Testes sizes (based on the gonad index) were relatively constant during spring and early summer, though they began to increase in size a month or two earlier than did the ovaries of females (Figure 7). During the constant period, they remained at minimum size, about 0.1% of body

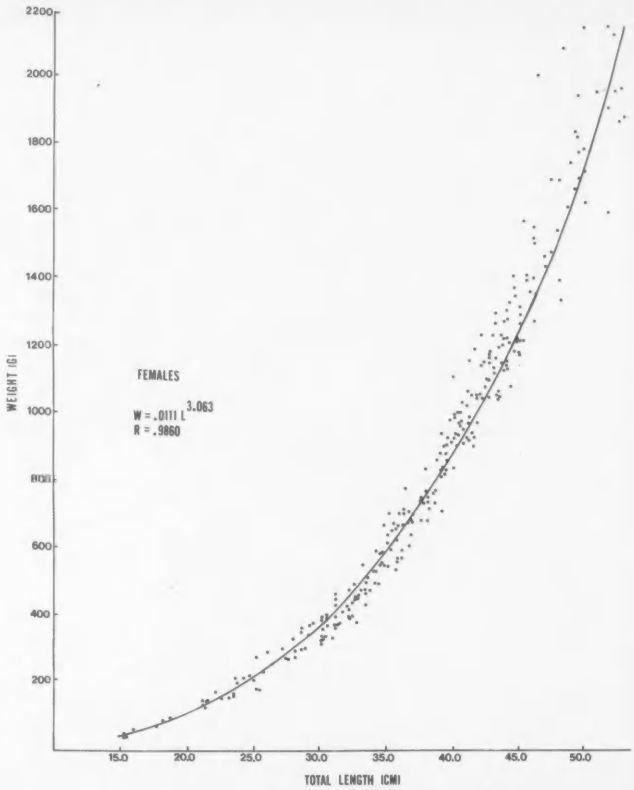

FIGURE 4.—Length-weight relationship based on 304 female olive rockfish sampled off Diablo Cove, 1972-77.

weight. They increased to 0.9-1.0% (maximum 2.2%) of body weight in late fall. It appeared that insemination occurred from October to December, perhaps peaking in November.

Moser (1967) found "a brood of advanced embryos or larvae and a series of ova undergoing vitellogenesis" in *S. chlorostictus*, *S. constellatus*, *S. eos*, *S. goodei*, *S. levis*, *S. ovalis*, *S. paucispinis*, and *S. rosaceus*, and stated that this offered direct evidence of multiple brood production. Similar findings for some of the above species were reported by MacGregor (1970), and Miller and Geibel (1973) noted that 1 of 648 *S. mystinus* examined showed multiple broods. We found no such evidence in olive rockfish, though females usually retained a few unexpelled eyed larvae, which appeared to be resorbed within a few months.

The evolution of reproductive isolating mechanisms in the genus *Sebastes* may not have included the restriction of random mating by seasonal isolation. It seems likely that the time from insemination to spawning is similar among closely related species. Rockfish species which mate over the same period, probably spawn at the same time during a later season. Olive rockfish and their presumed subgeneric congeners, *S. flavidus*, *S. mystinus*, and *S. melanops*, spawn and probably mate during the same seasons (Phillips 1964; Miller and Geibel 1973) as do other closely related rockfish species groups (e.g., *S. paucispinis-S. goodei*—Moser 1967) and other subgenera (*Sebastomus*—Chen 1971).

Instead, habitat isolation among some species (such as *S. chrysomelas-S. carnatus*—Larson 1977) may restrict interspecific mating. However, a number of species pairs (notably *S. paucispinis-S. goodei*) may aggregate together throughout the year. Even though closely related species mate in the same habitat, during the same season, hybrids

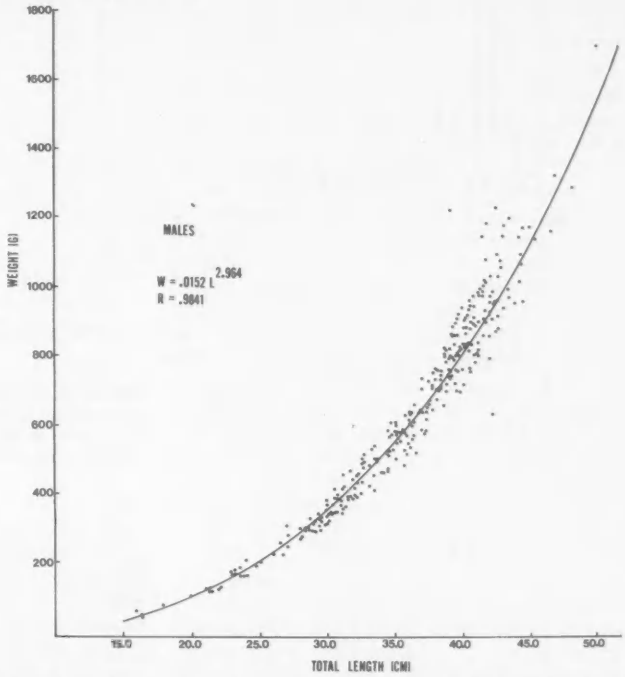

FIGURE 5.—Length-weight relationship based on 312 male olive rockfish sampled off Diablo Cove, 1972-77.

are very rare in California waters (the "hybrids" mentioned by Phillips (1964) are now recognized as distinct species), indicating that other antihybridization mechanisms are involved.

Though it is possible that extensive crossspecific mating occurs, and gametic or zygotic mortality prevents hybridization, it seems more likely that internal fertilization, necessitating close coordinated contact, has lent itself as a mechanism of mechanical and/or behavioral isolation. The copulatory organs of male *S. serranoides* are relatively small, thus a degree of closely coordinated movements is probably necessary to effect mating. Auditory, visual, and chemical cues may all play a part. It is known, for instance, that some rockfish species produce sounds (Hallacher 1974) and these may be used in species recognition. Deeper water species, living in relative darkness, may depend primarily on nonvisual recognition during mating season.

Size and Age at Maturity

It was often difficult to distinguish prereproductive female olive rockfish from mature late resting stage females (as noted by Westrheim 1975 and Gunderson 1977 in *S. alutus*). Females develop small orange ovaries 1 or 2 yr before they reproduce. During much of the year these "maturing" fish were easily distinguished from reproductive individuals by their consistently small, pale orange ovaries. However, during late spring and early summer, the ovaries of both reproductive and maturing fish are small and orange. Because mature and maturing females were not readily differentiated during late spring and early summer, females captured during this period were not included in this analysis.

There was considerable variation in size and age at first maturity (Figures 8, 9). A few fish were mature at 3 yr old (males 28.1-32.5 cm TL, females 31.1-33.6 cm TL). Yet not all males were mature before 7 yr and 39.0 cm TL, nor females before 8 yr and 37.0 cm TL. Over 50% of the females had spawned by 4 yr and 34.0 cm TL, while males were age 5 and 32.0 cm TL before reaching the 50% mark. In general, males first matured at a somewhat smaller size and somewhat later age than females.

Limbaugh (1955) reported that, off southern

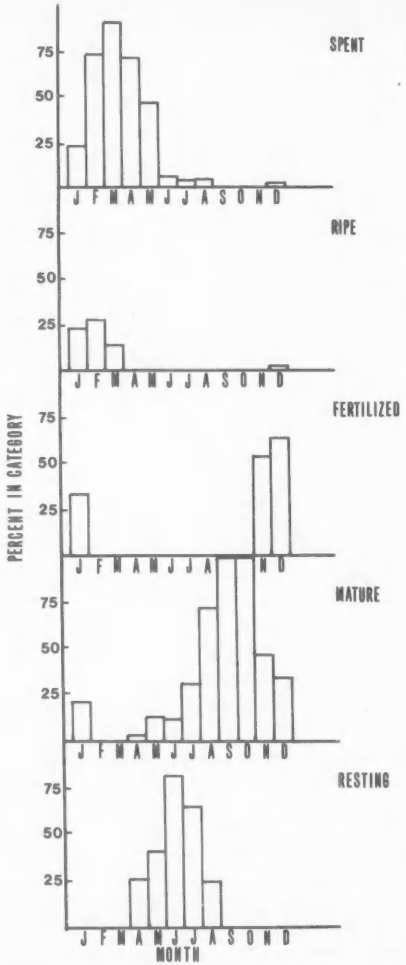

FIGURE 6.—Percent composition by month of five gonad condition stages for female olive rockfish taken off Diablo Cove, 1972-77. Resting refers to that period before egg development, vitellogenesis occurring during the maturing stage, which is terminated by the fertilized stage. Eyed larvae, which define ripe gonads, are extruded and the gonads are called spent.

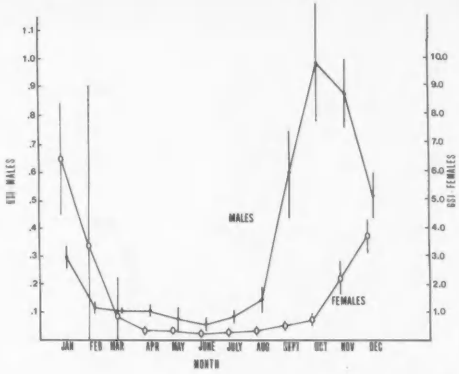

FIGURE 7.—Seasonal changes in the gonosomatic index (GSI—gonad weight as a percent of total body weight) of male and female olive rockfish. Vertical lines indicate 95% confidence intervals of the mean.

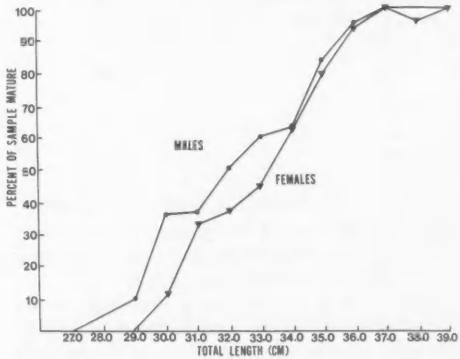

FIGURE 8.—Length-maturity relationship in 331 female and 318 male olive rockfish collected off Diablo Cove, 1972-77.

California, olive rockfish matured at 17-22 cm TL. This is considerably smaller than fishes taken off Diablo Cove. Unpublished data by Love (1978) indicated that olive rockfish off Santa Barbara (in southern California) mature at the same length as fishes farther north. It is possible that Limbaugh mistook prereproductive individuals, whose gonads do swell and color slightly, for mature fish.

Age of first maturity varies widely among rockfish species. At one extreme, *S. emphaeus* matures at 2-4 yr (Moulton 1975); *S. umbrosus*, *S. ensifer* (Chen 1971), and *S. jordani* (Phillips 1964) at 3 yr; while the others, *S. chlorostictus*, *S. rosenblatti*, and *S. constellatus* mature at about 10 yr (Chen 1971) and some stocks of *S. alutus* do not mature until 11 yr or later (Gunderson 1977). Modal period for first reproduction seems to be about 4-7 yr for most species (Phillips 1964; Patten 1973; Miller and Geibel 1973).

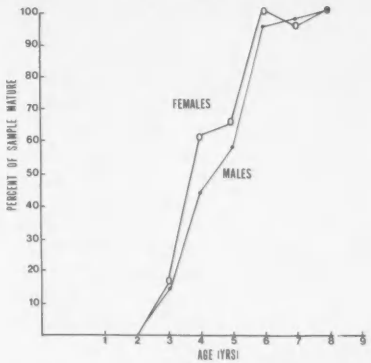

FIGURE 9.—Age-maturity relationship in 317 female and 302 male olive rockfish collected off Diablo Cove, 1972-77.

Fecundity

The nonlinear relation between fecundity and total length (Figure 10) was best described by the function $F = aL^b$, where F = number of eggs in thousands, L = total length in centimeters, and a and b = constants. The value of the parameters a and b were estimated by fitting the linear function $\log F = \log a + b \log L$ by least squares. Estimated fecundity ranged from 30,000 eggs for a 32.6 cm TL individual to about 490,000 for one 46.8 cm long.

Olive rockfish fecundity levels reflected the ranges determined for some other rockfish species, notably *S. flavidus* (Phillips 1964; Gunderson et al. 1980), *S. crameri*, *S. jordani*, and *S. entomelas* (Phillips 1964). They appear to be more fecund per body length than *S. alutus* (Gunderson 1977) and *S. goodei* (Phillips 1964; Gunderson et al. 1980) and less so than *S. elongatus*, *S. diploproa* (Phillips 1964), and *S. mystinus* (Miller and Geibel 1973). In all species studied, smaller individuals tend to carry fewer eggs. There is some evidence (MacGregor 1970) that smaller species also carry fewer eggs per body length.

Fish fecundity measurements, however, are tenuous at best and should only be looked upon as first approximations. Computations made before and after fertilization (Lisovenko 1956) or by differences in subsampling techniques (Gunderson 1977) may cause discrepancies between studies. Moreover the relationship between the number of maturing eggs in an ovary and viable larvae produced is unknown. Unfortunately, it is not practical to count larvae in the ovaries, as some may be lost during capture. Fecundity may also vary due to environmental factors (temperature—Rounsefell 1957 and food availability—Bagenal 1966) or genetic differences (Bagenal 1966).

Juveniles

Rockfish larvae are pelagic for a number of months, after which they settle into waters of various depths. The settling time and habitat of olive rockfish off Diablo Cove was determined from information based on underwater observations and young-of-the-year collected from 1974 to 1977. Though young *S. flavidus* closely resemble *S. serranoides*, and hence might be a source of confusion, they are rare in shallow waters off Diablo Cove (Berge and Schultz footnote 5). Based on spawning season and young-of-the-year sightings, olive rockfish probably spend 3-6 mo as pelagic larvae before settling out. Young-of-the-

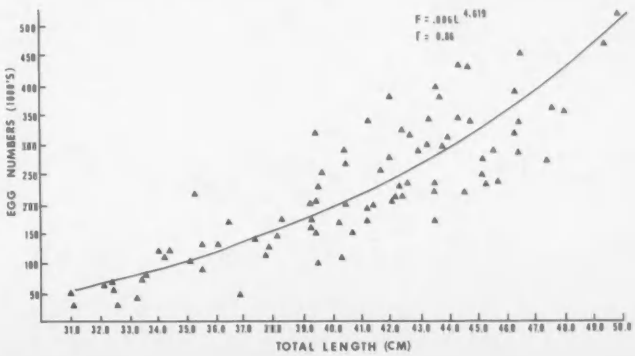

FIGURE 10.—Fecundity-total length relationship for 87 olive rockfish collected off Diablo Cove during October and November 1972-77.

year (of about 2-3 cm TL) first appeared inshore off Avila during March and April. At this stage, they were particularly common under the kelp canopy and over very shallow, protected rocky reefs (occasionally in the lower intertidal zone). Although they were not directly observed there, young-of-the-year probably also occur on reefs somewhat farther offshore (depth 20-50 m), since they were often found in the stomachs of resident rockfish in these habitats.

Food Habits

Olive rockfish were found to be primarily midwater predators of nekton (Table 5). Very important among its prey were small fishes, including blue rockfish; young olive rockfish; pipefish, *Syngnathus* sp.; shiner perch, *Cymatogaster aggregata*; kelp gunnel, *Ulvicola sanctaerosae*; northern anchovy, *Engraulis mordax*; topsmelt, *Atherinops affinis*; and cottids. Another important nektonic prey was the squid *Loligo opalescens*. Among planktonic prey, small crustaceans (particularly crab megalops larvae), tunicates (*Oikopleura* sp., *Doliolium* sp.), euphausids, fish larvae, and polychaetes were commonly eaten. Among substrate-oriented prey, octopus was the most important food item, followed by gammarid amphipods, isopod *Idothea* sp., and other small crustaceans.

As olive rockfish grow, their food habits change. Previous studies (Quast 1968b; Hobson and Chess 1976; Love and Ebeling 1978) have shown juvenile olive rockfish to be primarily midwater feeders, actively swimming after such forms as polychaetes, megalops larvae, mysids, and small fish. In the present study, though planktonic forms were important for individuals of all size classes, nektonic animals, primarily fish and squid, assumed dominance in the diet as the fish grew larger (Table 6). Plankton consumed by smaller individuals included a wide variety of small and large crustaceans, fish larvae, and polychaetes. For larger fish, plankton consumption was essentially limited to large items, such as euphausids, tunicates, and polychaetes. Nekton

TABLE 6.—Percentage occurrence of prey types in stomachs of four size classes (total length) of olive rockfish from Avila, Calif. Probabilities determined by 2 × 2 contingency *G*-test (Sokal and Rohlf 1969).

Size class (cm)	Stomachs with food (no.)	Plankton	Nekton	Substrate oriented
10.1-20.0	25	84.0*	16.0*	20.0
20.1-30.0	75	57.3*	40.0*	29.3
30.1-40.0	158	41.7**	56.5	22.0**
40.1-50.0	116	25.7	56.0	43.1

*$P \leq 0.05$, **$P \leq 0.01$.

TABLE 5.—Percentage total volume and frequency of occurrence of 17 food items in stomachs of olive rockfish off Avila, Calif. Olive rockfish are divided into 10.0 cm TL size groups. Food items are grouped by behavior and habitat.

	10.1-20.0 cm		20.1-30.0 cm		30.1-40.0 cm		40.1-50.0 cm		Total	
Food item by prey type	% vol	% freq	% vol	% freq	% vol	% freq	% vol	% freq	% vol	% freq
Primarily planktonic (sum)	(54.2)		(20.9)		(8.8)		(7.9)		(9.3)	
Small crustaceans, 0.5-5 mm:										
Zoea			.7	2.7	tr[1]	1.9			tr	1.3
Copepods	.8	24.0	1.2	4.0	tr	3.2	tr	1.7	tr	4.2
Megalops	4.8	28.0	9.6	33.3	.2	7.0	tr	3.4	.6	12.2
Large crustaceans, >10 mm:										
Euphausids			1.2	2.6	4.2	13.9	2.3	7.8	3.0	8.6
Small-medium sized, transparent										
Tunicates (salps, larvaceans)			.3	1.3	2.6	6.3	5.3	.9	4.0	5.7
Fish larvae	44.5	52.0	.9	6.6	.2	5.0	tr	1.7	.5	7.3
Polychaetes	4.1	16.0	7.0	28.0	1.6	22.8	.3	12.0	1.2	19.5
Primarily nektonic, 20-160 mm (sum)	(44.7)		(72.1)		(81.1)		(64.4)		(71.3)	
Fish	44.7	12.0	66.0	37.3	36.9	52.5	24.5	44.8	31.6	43.2
Squid			6.1	2.6	44.2	7.7	39.9	12.1	39.7	7.6
Primarily substrate oriented (sum)	(1.0)		(6.9)		(10.0)		(27.2)		(19.3)	
Free moving animals:										
Mysids			.9	4.0	tr	.6	tr	.9	tr	1.3
Isopods			.4	4.0	.3	6.0			.1	3.1
Gammaridean amphipods	1.0	20.0	2.2	18.6	.1	3.8	tr	.9	.2	6.8
Caprellid amphipods					tr	.6			tr	.2
Octopus			.7	2.6	9.3	12.0	27.2	37.9	18.6	16.7
Shrimp			.2	2.6					tr	.2
Algae			2.5	2.6	tr	1.9	tr	.9	.2	1.6
Pebbles					.3	1.3	tr	.9	.2	.8
Total volume of food consumed, ml	15.58		101.34		840.82		1,162.65		2,120.39	
Stomachs with food, no.	25		75		158		116		374	
Empty stomachs, %	22.0		33.0		38.3		39.3			

[1]Trace <0.05%.

feeding, though important in all size classes, increased to a peak for fish 30.1-40.0 cm long, then declined somewhat, as larger fish ate more substrate-oriented prey. Predators in the 20.1-30.0 cm size class had the smallest range of food items (Table 7), eating mostly fish. Range increased for larger predators, as their diets were supplemented by squid and octopus.

TABLE 7.—Food breadths (Bray and Ebeling 1975) based on proportionate item volumes for four size classes (total length) of olive rockfish from Avila, Calif. Maximum vol (%) is of the dominant item (Table 5).

Size class (cm)	Stomachs with food (no.)	Food items eaten (no.)	Breadth of diet	Maximum vol (%)	Dominant item
10.1-20.0	25	6	2.49	44.7	Fish
20.1-30.0	75	15	2.20	43.6	Fish
30.1-40.0	158	16	2.92	44.2	Squid
40.1-50.0	116	13	3.40	39.9	Squid

Feeding on substrate-oriented forms, primarily gammarid amphipods and isopods, occurred occasionally in fish of the smaller size classes, but was much more frequent in larger fish, where foraging on octopus was important. Octopuses are normally secretive during daylight hours, but are often exposed during the night (D. Behrens[6]). Olive rockfish may feed at night on octopus—an example of a fish not adapted to benthic feeding, preying successfully on a bottom-dwelling form.

Food habits showed some seasonal variation. Nekton feeding significantly increased (in the 30.1-40.0 and 40.1-50.0 cm size classes) during the upwelling period (Table 8). Predation on both squid and young-of-the-year rockfish (which first appear in large numbers during April and May) increased during this period. Though juvenile rockfish were an important food item throughout the year, their importance decreased during fall and winter, probably because these growing juveniles become less vulnerable. Other prey, such as the northern anchovy, were of greater importance during the fall oceanic and winter Davidson Current periods. Tunicates and euphausids were eaten in far greater amounts during the upwelling season, particularly during April and May (an occurrence also noted off Carmel Bay, Calif., by Roberts 1979).

Limbaugh (1955) speculated that olive rockfish may replace kelp bass ecologically in central and northern California, where kelp bass decline in abundance. The two species are similar in appearance—having elongate, fusiform bodies, reduced or (in kelp bass) absent head spines, large mouths, and brownish bodies with light blotches along their back. In central and northern California, olive rockfish do, to a certain degree, assume the lifestyle of kelp bass. Olive rockfish live over high relief bottom and feed primarily on nekton, as do kelp bass. However, with the exception of octopus, olive rockfish rarely prey on the substrate-oriented food items, such as shrimp, algae, and hydroids, favored by kelp bass (Quast 1968b; Love and Ebeling 1978). In central California, olive rockfish and blue rockfish are the major midwater predators over inshore reefs. Though there is considerable overlap, blue rockfish feed primarily on relatively slow moving or drifting prey, such as tunicates, copepods, and chaetognaths (Gotshall et al. 1965; Hallacher 1977) while olive rockfish concentrate on more motile forms. Beginning in northern California, olive rockfish give way to midwater feeding yellowtail rockfish and black rockfish, *S. melanops* (Moulton 1977).

TABLE 8.—Seasonal variation in percentage frequency of occurrence of prey types in stomachs of three size classes (total length) of olive rockfish from Avila, Calif. Seasonal periods are explained in the text. Probabilities determined by 2 × 2 contingency G-test (Sokal and Rohlf 1969) on original frequencies.

Size class	Prey type	Seasonal period: Mar.-Aug.	Seasonal period: Sept.-Feb.
20.1-30.0 cm:			
Stomachs with food, no.		38	37
	Plankton, %	47.4	64.9
	Nekton, %	39.5	51.4
	Substrate oriented, %	31.6	21.6
30.1-40.0 cm:			
Stomachs with food, no.		71	87
	Plankton, %	42.3	46.0
	Nekton, %	70.4*	50.6
	Substrate oriented, %	19.7	23.0
40.1-50.0 cm:			
Stomachs with food, no.		63	53
	Plankton, %	30.2	22.6
	Nekton, %	66.7**	45.3
	Substrate oriented, %	39.7	45.3

*$P \leq 0.05$
**$P \leq 0.01$

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[6]D. Behrens, Pacific Gas and Electric, Biological Laboratory, P.O. Box 117, Avila, CA 93424, pers. commun. November 1980.

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LITERATURE CITED

ALLEN, R. L.
1976. Method for comparing fish growth curves. N.Z. J. Mar. Freshwater Res. 10:687-692.

BAGENAL, T. B.
1966. The ecological and geographical aspects of the fecundity of the plaice. J. Mar. Biol. Assoc. U.K. 46:161-186.

BAGENAL, T. B., AND E. BRAUM.
1971. Eggs and early life history. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, p. 166-198. IBP (Int. Biol. Programme) Handb. 3.

BAKUN, A.
1973. Coastal upwelling indices, west coast of North America, 1946-71. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-671, 96 p.

BRAY, R. N., AND A. W. EBELING.
1975. Food, activity, and habitat of three "picker-type" microcarnivorous fishes in the kelp forests off Santa Barbara, California. Fish. Bull., U.S. 73:815-829.

CARLSON, H. R., AND R. E. HAIGHT.
1972. Evidence for a home site and homing of adult yellowtail rockfish, *Sebastes flavidus*. J. Fish. Res. Board Can. 29:1011-1014.

CHEN, L.-C.
1971. Systematics, variation, distribution, and biology of rockfishes of the subgenus *Sebastomus* (Pisces, Scorpaenidae, *Sebastes*). Bull. Scripps Inst. Oceanogr. Univ. Calif. 18, 115 p.

DARK, T. A.
1975. Age and growth of the Pacific hake, *Merluccius productus*. Fish. Bull., U.S. 73:336-355.

FRAIDENBURG, M. E.
1980. Yellowtail rockfish, *Sebastes flavidus*, length and age composition off California, Oregon, and Washington in 1977. Mar. Fish. Rev. 42(3-4):54-56.

GOTSHALL, D. W., J. G. SMITH, AND A. HOLBERT.
1965. Food of the blue rockfish *Sebastodes mystinus*. Calif. Fish Game 51:147-162.

GUNDERSON, D. R.
1977. Population biology of Pacific ocean perch, *Sebastes alutus*, stocks in the Washington-Queen Charlotte Sound region, and their response to fishing. Fish. Bull., U.S. 75:369-403.

GUNDERSON, D. R., P. CALLAHAN, AND B. GOINEY.
1980. Maturation and fecundity of four species of *Sebastes*. Mar. Fish. Rev. 42(3-4):74-79.

HALLACHER, L. E.
1974. The comparative morphology of extrinsic gasbladder musculature in the scorpionfish genus *Sebastes* (Pisces: Scorpaenidae). Proc. Calif. Acad. Sci. 40:59-86.
1977. Patterns of space and food use by inshore rockfishes (Scorpaenidae:*Sebastes*) of Carmel Bay, California. PhD Thesis, Univ. California, Berkeley, 115 p.

HOBSON, E. S., AND J. R. CHESS.
1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. Fish. Bull., U.S. 74:567-598.

LARSON, R. J.
1977. Habitat selection and territorial competition as the causes of bathymetric segregation of sibling rockfishes (*Sebastes*). PhD Thesis, Univ. California, Santa Barbara, 170 p.

LEA, R. N., AND J. E. FITCH.
1979. A new species of rockfish, genus *Sebastes* (Scorpaenidae), from the eastern North Pacific off Mexico and California. Nat. Hist. Mus. Los Ang., Contr. Sci. 320, 7 p.

LIMBAUGH, C.
1955. Fish life in the kelp beds and the effects of kelp harvesting. Univ. Calif., Inst. Mar. Res. Ref. 55-9, 158 p.

LISOVENKO, L. A.
1956. Fecundity of *Sebastodes alutus* Gilbert, in the Gulf of Alaska. Tr. Vses. Nauchno-Issled. Morsk. Rybn. Khoz. Okeanogr. 58 (Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. 53):171-178. (Transl. 1968. *In* P. A. Moissev (editor), Soviet fisheries investigations in the Northeast Pacific, Part 4, p. 162-169, available Natl. Tech. Inf. Serv., Springfield, Va., as TT 67-51206.)

LOVE, M. S.
1978. Aspects of the life history of the olive rockfish, *Sebastes serranoides*. PhD Thesis, Univ. California, Santa Barbara, 185 p.
1980. Isolation of olive rockfish, *Sebastes serranoides*, populations off southern California. Fish. Bull., U.S. 77:975-983.

LOVE, M. S., AND A. W. EBELING.
1978. Food and habitat of three switch-feeding fishes in the kelp forests off Santa Barbara, California. Fish. Bull., U.S. 76:257-271.

MACGREGOR, J. S.
1970. Fecundity, multiple spawning and description of the gonads in the *Sebastodes*. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 596, 12 p.

MILLER, D. J., AND J. J. GEIBEL.
1973. Summary of blue rockfish and lingcod life histories; a reef ecology study; and giant kelp, *Macrocystis pyrifera*, experiments in Monterey Bay, California. Calif. Dep. Fish Game, Fish Bull. 158, 137 p.

MILLER, D. J., AND D. GOTSHALL.
1965. Ocean sportfish catch and effort from Oregon to Point Arguello, California. Calif. Dep. Fish Game, Fish Bull. 130, 135 p.

MOSER, H. G.
1967. Reproduction and development of *Sebastodes paucispinis* and comparison with other rockfishes off southern California. Copeia 1967:773-797.

MOULTON, L. L.
1975. Life history observations on the Puget Sound rockfish, *Sebastes emphaeus* (Starks, 1911). J. Fish. Res. Board Can. 32:1439-1442.
1977. An ecological analysis of fishes inhabiting the rocky

nearshore regions of northern Puget Sound, Washington. PhD Thesis, Univ. Washington, Seattle, 181 p.

PACIFIC MARINE FISHERIES COMMISSION.
1980. 32nd Annual Report of the Pacific Marine Fisheries Commission for the year 1979. Portland, Oreg., 49 p.

PATTEN, B. G.
1973. Biological information on copper rockfish in Puget Sound, Washington. Trans. Am. Fish. Soc. 102:412-416.

PHILLIPS, J. B.
1964. Life history studies on ten species of rockfish. Calif. Dep. Fish Game, Fish Bull. 126, 70 p.

PINKAS, L.
1977. California marine fish landings for 1975. Calif. Dep. Fish Game, Fish Bull. 168, 55 p.

QUAST, J. C.
1968a. Fish fauna of the rocky inshore zone. *In* W. J. North and C. L. Hubbs (compilers and editors), Utilization of kelp-bed resources in southern California, p. 35-55. Calif. Dep. Fish Game, Fish Bull. 139.
1968b. Observations on the food of the kelp-bed fishes. *In* W. J. North and C. L. Hubbs (compilers and editors), Utilization of kelp-bed resources in southern California, p. 109-142. Calif. Dep. Fish Game, Fish Bull. 139.

ROBERTS, D. A.
1979. Food habits as an ecological partitioning mechanism in the nearshore rockfishes (*Sebastes*) of Carmel Bay, California. Masters Thesis, San Francisco State Univ., 74 p.

ROUNSEFELL, G. A.
1957. A method of estimating abundance of groundfish on Georges Bank. U.S. Fish Wildl. Serv., Fish. Bull. 57: 265-278.

SIX, L. D., AND H. F. HORTON.
1977. Analysis of age determination methods for yellowtail rockfish, canary rockfish, and black rockfish off Oregon. Fish. Bull., U.S. 75:405-414.

SOKAL, R. R., AND F. J. ROHLF.
1969. Biometry; the principles and practice of statistics in biological research. W. H. Freeman, San Franc., 776 p.

WESTRHEIM, S. J.
1973. Age determination and growth of Pacific ocean perch (*Sebastes alutus*) in the northeast Pacific Ocean. J. Fish. Res. Board Can. 30:235-247.
1975. Reproduction, maturation, and identification of larvae of some *Sebastes* (Scorpaenidae) species in the northeast Pacific Ocean. J. Fish. Res. Board Can. 32: 2399-2411.

WILKINS, M. E.
1980. Size composition, age composition, and growth of chilipepper, *Sebastes goodei*, and bocaccio, *S. paucispinis*, from the 1977 rockfish survey. Mar. Fish. Rev. 42(3-4): 48-53.

WILLIAMS, T., AND B. C. BEDFORD.
1974. The use of otoliths for age determination. *In* T. B. Bagenal (editor), The aging of fish, p. 114-123. Unwin Brothers Limited, Surrey.

WISHARD, L. N., F. M. UTTER, AND D. R. GUNDERSON.
1980. Stock separation of five rockfish species using naturally occurring biochemical genetic markers. Mar. Fish. Rev. 42(3-4):64-73.

OVARIAN CYCLING FREQUENCY AND BATCH FECUNDITY IN THE QUEENFISH, *SERIPHUS POLITUS*: ATTRIBUTES REPRESENTATIVE OF SERIAL SPAWNING FISHES

E. E. DeMartini and Robert K. Fountain[1]

ABSTRACT

Egg production by *Seriphus politus* near San Diego in southern California was studied during 1978-79. Spawning frequency was estimated on the basis of incidence of females with hydrated eggs. Estimates of annual egg production were an order of magnitude greater than estimates based on conventional methods.

Seriphus politus spawns during March-August, and females mature at 10.0-10.5 cm standard length in their first spring or second summer following birth. Planktonic eggs are spawned between late afternoon and early evening. Spawning is asynchronous among females, but has monthly peaks in intensity during the waxing (first quarter) of the moon. Fecundity is proportional to size and is better correlated with weight than with length of female. Individuals spawn once a week on average, regardless of body size. Larger females begin spawning earlier in the season and continue spawning after the smallest females have ceased. Recruit spawners and the largest repeat spawners produce about 12 to 24 batches of eggs during their respective spawning seasons. The average-sized female spawns about 300,000 eggs in a year. Relative fecundity is an increasing function of body size. Larger females produce larger eggs, and all females produce larger eggs earlier in the season. Implications of these life-history attributes are discussed.

The croakers (family Sciaenidae) are a major component of the nearshore fish fauna of southern California (Frey 1971), yet little is known about their fecundity patterns or other details of their reproductive biology (Skogsberg 1939). Seven species of croakers occur off southern California (Miller and Lea 1972). General information on breeding seasonality and size at sexual maturity exists for white seabass, *Atractoscion nobilis* (Clark 1930); black croaker, *Cheilotrema saturnum* (Limbaugh 1961; Fitch and Lavenberg 1975); California corbina, *Menticirrhus undulatus* (Fitch and Lavenberg 1971; Frey 1971); and spotfin croaker, *Roncador stearnsi* (Frey 1971). The general seasonal nature of spawning is known for yellowfin croaker, *Umbrina roncador* (Frey 1971). Additional data on ovarian cycling exist only for white croaker, *Genyonemus lineatus*, and for queenfish, *Seriphus politus* (Goldberg 1976).

The queenfish is an abundant, small species that is a major component of the sport fish catch on piers in southern California (Frey 1971); the species moreover provides forage for several fishes important to the sport and commercial fisheries in the area (Young 1963; Feder et al. 1974). It is the purpose of this paper to document the fecundity and ovarian cycling patterns of queenfish and to relate these results to what we feel are some general reproductive characteristics of serial spawning fishes.

MATERIALS AND METHODS

Field Sampling

Fish were sampled at nearshore (5-20 m) depths, 0.5-3 km from shore, between San Clemente and Oceanside, Calif. (Figure 1), using a lampara net (560 m long × 25 m deep, mesh: 15 cm in wings to 1.25 cm in center bag), fished surface-to-bottom by a commercial vessel. Fish were caught at standard times of day (1-6 h after dawn) and night (1-6 h after sunset) on surveys conducted at fortnightly (September 1978-February 1979; September 1979) or weekly (March-August 1979) intervals. Six daytime and five nighttime net hauls were made each survey.

[1]Marine Science Institute, University of California, Santa Barbara, CA 93106.

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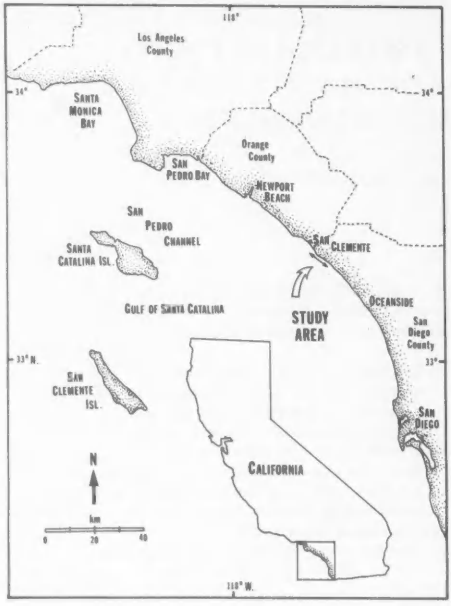

FIGURE 1.—Map of the study area.

Analysis of Fish and Ovaries

A maximum of two aliquots of 50 fish each were sacrificed from each net haul to determine size (standard length, SL, in millimeters) and sex composition. At most 15 females per 5 mm length class in each haul were measured and their ovaries excised and weighed (0.01 g) while fresh. Fresh (ovary-free) body weight (0.1 g) was recorded for subsampled, mature fish of a range of lengths. One or both ovaries of each mature pair were fixed and preserved in modified Gilson's fluid (Bagenal and Braum 1971) for 1-3 mo. Gonads were classified either as immature or mature according to several gross criteria (vascularization, oocyte appearance, Table 1) of Bagenal and Braum (1971). Gonad maturity also was estimated using a gonad index, $GI = W/SL^3 \times C$ (Moser 1967), where W = weight of both ovaries in grams, SL = standard length in millimeters, and the constant $C = 10^8$. The median diameter (random axis) was determined for oocytes present in the largest size-frequency mode in ripening ovaries (Stage 2, Table 1) of each of 10-15 fish from pooled monthly samples. Oocyte maturation size was inferred from a plot of median oocyte diameter versus gonad index (Higham and Nicholson 1964). For select ripe (Stage 3, Table 1) females, both ovaries were reweighed after Gilson's preservation, a tissue sample ($\bar{X} = 3.4 \pm 1.0\%$ (SE), range 1.0-7.2% of the weight of both ovaries) weighed, and the numbers of oocytes in the largest size-frequency mode estimated for both ovaries by gravimetric method (Bagenal and Braum 1971). Tissue samples from either ovary of a pair were used, as the right and left ovaries of *S. politus* are, on average, equivalent in weight (paired t-test, n = 20 ovary pairs, $0.4 > P > 0.3$) and in the size-frequency distribution of oocytes (Kolmogorov-Smirnov 2-sample test, $n = 5$ ovary pairs, $P > 0.1$). Tissue samples for fecundity analysis were taken from the anterior one-third of the ovary. For other select Stage 2 and 3 fish, the second ovary of a pair was fixed in 10% Formalin[2] for 2 wk, sectioned at 0.008 mm, stained with Harris' hematoxylin and eosin, and a slide mount examined at 60-240× to validate classification as nonhydrated or hydrated based on the gross ovarian characteristics listed in Table 1. The latter tissue samples were also taken from the anterior one-third of the ovary. No difference existed in the frequency distribution of oocyte maturation states within anterior, central, or posterior regions of the queenfish ovary (Smirnov 3-sample test, $n = 5$ ovary pairs, $P > 0.1$; Conover 1971).

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Gross characteristics of various stages in the queenfish ovarian cycle.

Egg stages within the ovary		Gross appearance of ovary and oocytes
1	Vestigial (= immature or inactive)	Ovaries avascular; oocytes not visible to naked eye. Ovaries uniform whitish-yellow.
2	Nonhydrated (= ripening)	Ovaries vascular and oocytes visible to the naked eye. Oocytes uniformly small, opaque, and straw-yellow throughout entire ovary.
3	Hydrated (= ripe)	Many small, opaque oocytes plus a minority of large, hyaline oocytes present throughout ovary. The two egg types together produce a speckled, translucent-opaque appearance, yellowish-orange to orange, throughout ovary.
4	Ovulated (= running)	A band of small, opaque, straw-yellow oocytes present along dorsal ridge of ovary; many large, hyaline oocytes visible within lumen of ovary. Most of ovary uniform yellowish-orange or orange.
5	Residual (= spent)	Ovary slightly blood-shot and deflated (partially spent) to very blood-shot, completely collapsed and flaccid (totally spent). A small number of large, ovulated eggs usually visible in lumen of ovary. Most oocytes present are small and opaque.

RESULTS

Spawning Season and Gonad Maturation

Queenfish ovaries accelerate development in February when daylight lengthens beyond 10 h and nearshore water temperatures are 15°-16° C. Ovaries increase to their maximum relative weight in April-May and decline through August until a resting stage recurs in September (Figure 2A). During February-September, nearshore water temperatures in general increase to 17°-19° C, although aperiodic bouts of upwelling (13°-14° C water) occur (J. Reitzel[3]). Ovaries mature at a GI of 40, when the diameter of Gilson's fluid-fixed (nonhydrated) oocytes reaches 350 μm (Figure 3).

Body Size and Time of Spawning

The first sexual maturation of females begins at a length of 10-10.5 cm. The proportion of sexually active females increases with body size until, at a length of about 12 cm SL, virtually all females are spawning by midseason (Table 2). Larger females (>12 cm, age II and older, DeMartini et al.[4]) start spawning earlier and finish spawning later in the year than fish ≤12 cm SL (Table 2, Figure 4). Duration of spawning varies from 3 mo for first

[3]Reitzel, J. 1979. Physical/chemical oceanography. *In* Interim Report of the Marine Review Committee of the California Coastal Commission. Part II: Appendix of Technical Evidence in Support of the General Summary, March 12, 1979, p. 6-23. Unpubl. rep. Marine Review Committee Research Center, 533 Stevens Avenue, Suite E-36, Solana Beach, CA 92075.

[4]DeMartini, E. E., K. M. Plummer, and T. O. Moore. Age and growth of the queenfish (*Seriphus politus*), with back-calculated length-at-age estimates based on sections of otolith sagittae. Manuscr. in prep. Marine Science Institute, Univ. Calif., Santa Barbara, CA 93106.

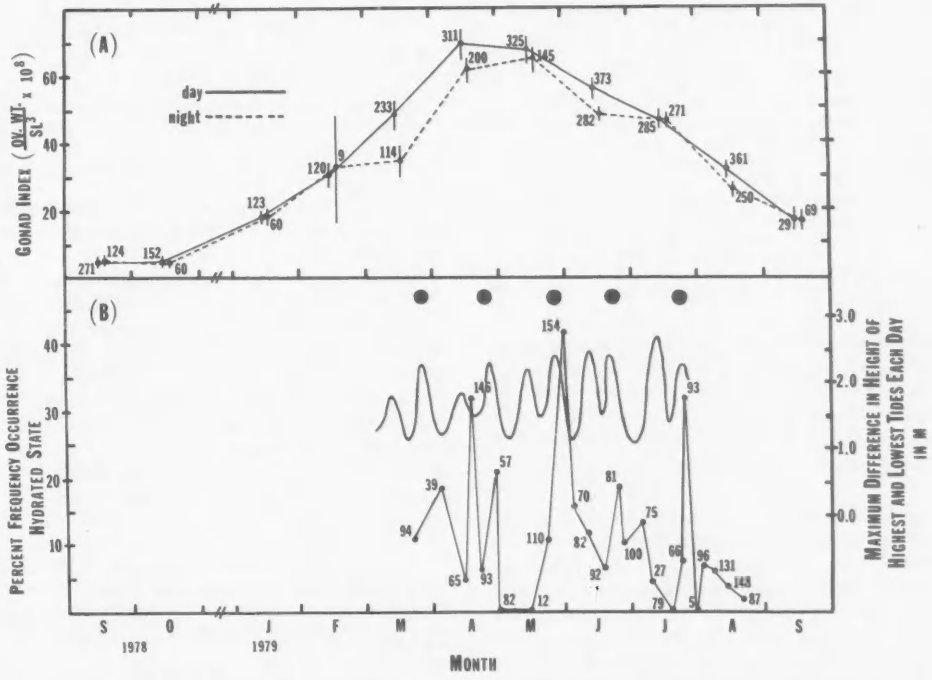
(A)
day
night
GONAD INDEX (GW. WT. / SL³ x 10⁸)
(B)
PERCENT FREQUENCY OCCURRENCE HYDRATED STATE
MAXIMUM DIFFERENCE IN HEIGHT OF HIGHEST AND LOWEST TIDES EACH DAY IN M
S O J F M A M J J A S
1978
1979
MONTH

FIGURE 2.—(A) Mean gonad indices of female queenfish (of all body sizes) collected September 1978-September 1979. Indices of day and night sample fish plotted separately. Sample sizes and 95% confidence limits are indicated. (B) Percent frequency occurrence of adult female queenfish with ovaries containing oocytes in hydrated condition during March-August 1979. Fish are from daytime collections at 5-11 m depths. Noted are the numbers of sample fish, dates of new moon, and maximum range in heights of highest and lowest tides each day.

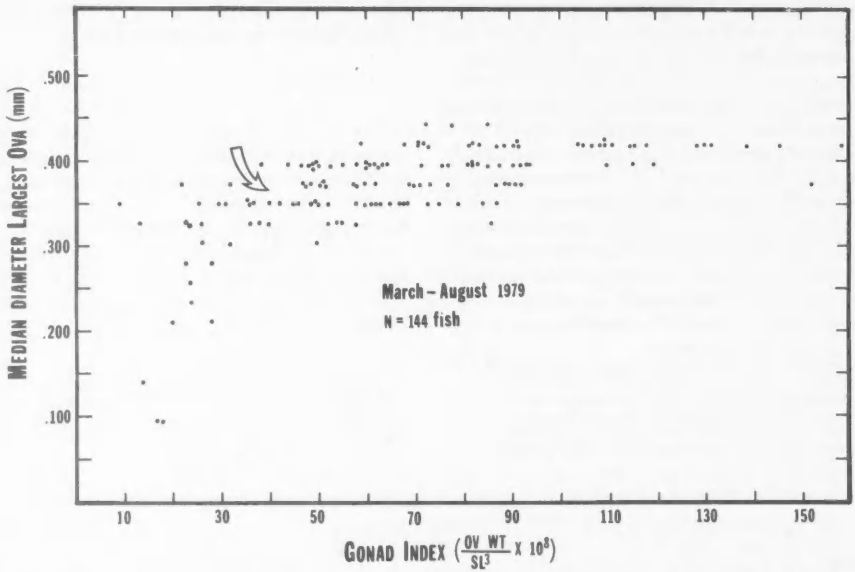

FIGURE 3.—Scattergraph of the median diameter (random axis) of the largest size-frequency mode of oocytes plotted against gonad index of the respective female queenfish. Asymptote (noted by arrow) occurs at an oocyte diameter of about 350 μm, corresponding to a gonad index of about 40.

TABLE 2.—Percent of female queenfish of various length classes[1] that were sexually mature during the 1979 spawning period.

Length class (cm SL)	Percent mature					
	Mar.	Apr.	May	June	July	Aug.
<10.5	0	0	<1	2	3	<1
10.6-11.0	14	63	68	58	22	3
11.1-11.5	18	95	93	92	53	9
11.6-12.0	48	97	100	94	85	12
12.1-12.5	82	98	100	100	96	73
12.6-13.0	90	100	100	98	99	97
13.1-13.5	100	100	100	98	100	100
>13.5	100	100	100	100	>97	>99

[1]An average of 90 female queenfish per length class were examined each month.

spawners to 6 mo in the largest fish. Relatively few females start spawning at age I. Of all sexually active (Stages 2-4, Table 1) females captured during the 1979 spawning season, 6 and 34% were <12 cm and <13.5 cm, respectively.

Ovarian Cycling

Monthly peaks in the proportion of females in ready-to-spawn condition occurred during the moon's first quarter (contingency chi square = 27.7; 3 df; $P<0.0005$; Siegel 1956). At such times from 19 to 42% of all the adult females in the day's samples had ovaries containing eggs in a hydrated state (Figure 2B).

Female *S. politus* begin hydrating oocytes after dawn and spawn between late afternoon and evening. No difference existed between the percent frequency occurrence of ready-to-spawn females in samples collected at different times during daylight hours; and no fish caught at any time during the night were ready to spawn (Table 3). These results were reexamined for subsample ovaries, using accepted histological criteria for distinguishing hydrated from non-

TABLE 3.—Frequency occurrence of mature female queenfish whose ovaries contained oocytes in a hydrated vs. a nonhydrated state in samples collected during various 6-h intervals on 25-28 June 1979.

Collection period	No. samples	No. fish containing		No. females examined
		Hydrated oocytes	Nonhydrated oocytes only	
0600-1200	3	10	90	100
1200-1800	4	15	66	81
1800-0000	5	0	81	81
0000-0600	5	0	84	84

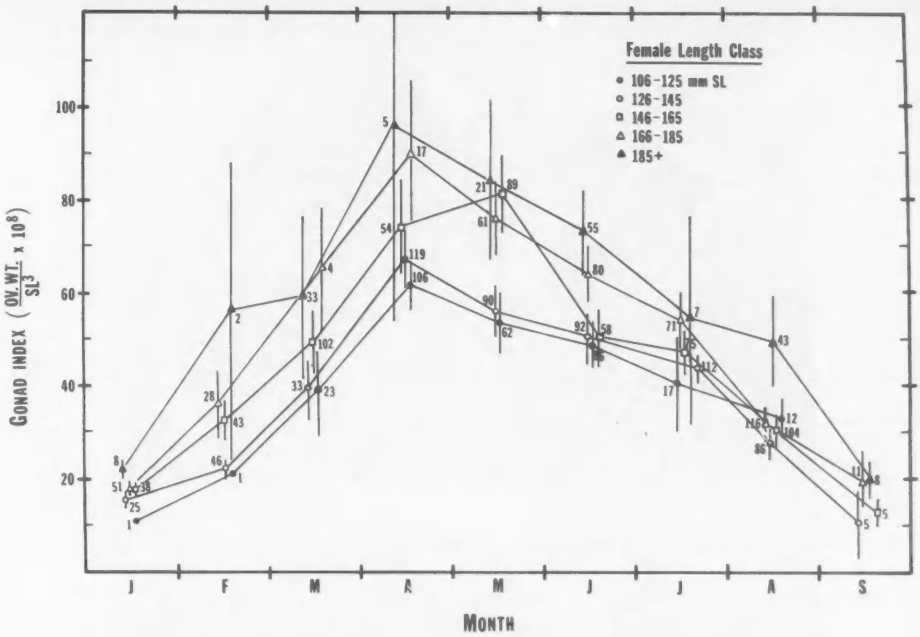

FIGURE 4.—Mean gonad indices of adult female queenfish of five length classes collected March-August 1979. Sample sizes and 95% confidence limits of means are indicated.

hydrated oocytes (Yamamoto and Yamazaki 1961; Yamamoto and Yoshioka 1964; Macer 1974; Htun-Han 1978), as illustrated in Figure 5. Histological results verified our conclusions based on the external appearance of ovaries (Table 4).

Spawning frequency thus can be inferred from the proportion of daytime sample fish whose ovarian eggs are in a hydrated state. Throughout the 1979 spawning season, an average of 13.6% of the females (of all sizes) present in daytime samples were in a ready-to-spawn condition (Table 5); thus females spawn on average every 7.4 d. Spawning frequency was similar for females of all body sizes (Table 5). Confidence intervals of these percent frequency occurrence data are necessarily asymmetrical, since female spawners are contagiously distributed among sample fish and, like hydrated-state females of the northern anchovy, *Engraulis mordax* (Hunter and Goldberg 1980), their sampling frequency is best described by the normal-log negative binomial distribution.

Sex Ratio

The breeding adult sex ratio of *S. politus* was 1.04 males to 1.00 females. The mean percentage of females among 16,794 adults was 49% with a 95% confidence interval of ±0.8%. The sex ratio was more skewed in favor of males in samples of fish containing one or more females in ready-to-spawn condition (Table 6).

Batch Fecundity

The number of eggs liable to be produced per spawning, i.e., the potential batch fecundity, was estimated for fish collected throughout the 1979 spawning season. The Gilson's fluid-fixed ovaries of daytime sample fish of a complete range of body sizes were used. Potential fecundity varied as the cube of standard length, and was proportional to body size in a consistent manner throughout the season (Figure 6). Bimonthly regressions of

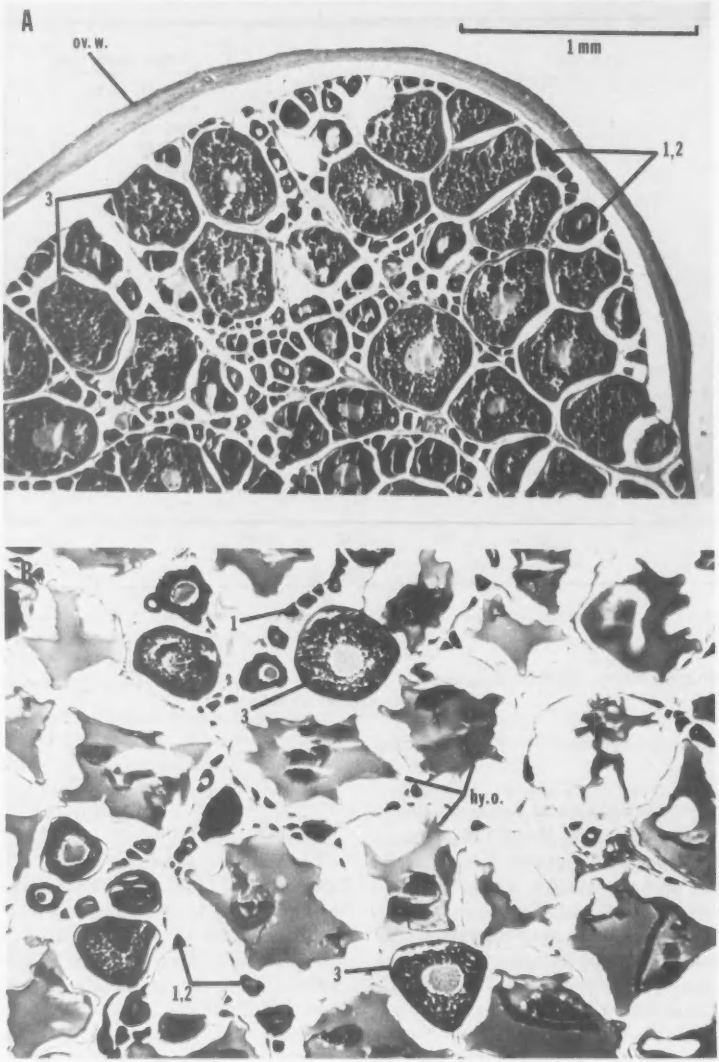

FIGURE 5.—Photomicrographs of transverse sections of (A) Stage 2 and (B) Stage 3 mature queenfish ovaries. Hyaline (hydrated) oocytes are still in their follicles in (B). Key for plate: hy.o. - hyaline oocyte; 1, 2 - Type 1 or Type 2 developing oocyte; 3 - Type 3 developing oocyte; ov.w. - ovarian wall. [See Goldberg (1976) for definitions and histological criteria distinguishing the stages of oocyte development in queenfish.]

TABLE 4.—Agreement between queenfish ovaries classified as hydrated or nonhydrated using external (gross) appearance and histological (microscopic) techniques.[1]

		Microscopic basis	
		Hydrated	Nonhydrated
Gross basis	Hydrated	49	2
	Nonhydrated	2	60

[1]n = 113 ovary pairs scored as (non)hydrated prior to fixation, staining, sectioning, and microscopic examination.

TABLE 5.—Frequency occurrence of queenfish ovaries in hydrated condition[1] as percent of all ovaries from adult sample fish[2] collected March-August 1979. The 95% confidence intervals on the percentage of hydrated females are indicated in parentheses.

Size group (cm SL)	No. sample fish	No. nonhydrated	No. hydrated	Mean[3] percent hydrated
10.5-12.5	342	294	48	14.0 (6.8, 28.8)
12.6-14.5	608	525	83	13.6 (7.9, 23.5)
14.6-16.5	519	462	57	11.0 (7.5, 16.1)
16.6-18.5	450	384	66	14.7 (6.8, 31.9)
>18.5	156	128	28	17.9 (9.0, 35.4)
All sizes	2,075	1,793	282	13.6 (8.2, 22.7)

[1]Classified based on gross characteristics of ovaries.
[2]Four net haul samples (daytime, 5-11 m) collected on 1 d cruise each week during 22 March-20 August 1979.
[3]Calculations based on normal-log negative binomial distribution (Zweifel and Smith in press).

fecundity on body size neither varied in slope (F = 1.49; 2,136 df; $P>0.25$) nor in intercept (F = 0.50; 2,138 df; $P>0.75$). Data were thus pooled over the entire 6-mo season and the general fecundity-length relation described by the best fit (R^2 = 0.664, n = 142, $P<0.01$) equation

$$\log_{10} F = 3.3809 \log_{10} SL - 3.1455$$

where F = batch fecundity
SL = standard length in millimeters.

Fecundity was better correlated (R^2 = 0.816, n = 42) with body weight (Figure 7) than with length of female (Figure 6), as described by the equation

$$\log_{10} F = 1.302 \log_{10} W + 1.968$$

where W = ovary-free weight in grams.

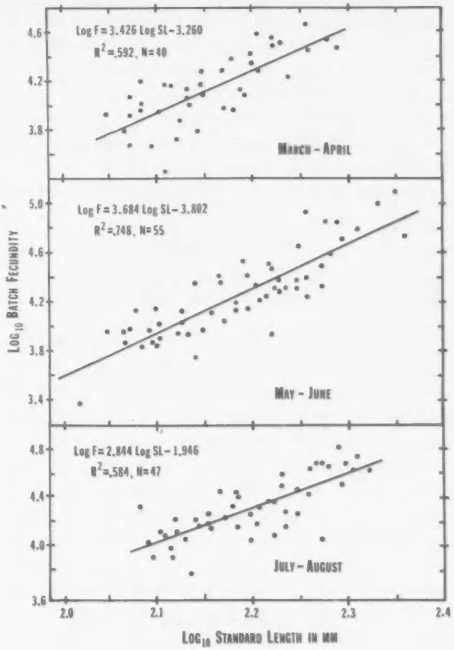
Log F = 3.426 Log SL - 3.260
R² = .592, N = 40
March - April
Log F = 3.684 Log SL - 3.802
R² = .748, N = 55
May - June
Log F = 2.844 Log SL - 1.946
R² = .584, N = 47
July - August
Log10 Batch Fecundity
Log10 Standard Length in mm

FIGURE 6.—Relation between the common logarithms of batch fecundity (as the number of hydrating oocytes) and length of queenfish collected during the first, middle, and latter third of the 1979 spawning season. Regression equations are least squares best fit.

The length-weight relation was tightly correlated (R^2 = 0.986, n = 175) according to the equation

$$\log_{10} W = 3.1105 \log_{10} SL - 5.0560.$$

The average-sized (14 cm, 42 g) female had a potential batch fecundity during 1979 of 12,000-13,000 eggs. Batch fecundities ranged from about 5,000 eggs in a 10.5 cm female to about 90,000 eggs in a 25 cm fish.

TABLE 6.—Relation between adult sex ratio (females/total adults) of samples and percent frequency occurrence of female queenfish containing hydrated[1] eggs.

Sex ratio class	Class mean	No. samples[2]	Percent of females containing: Hydrated[1] eggs	Percent of females containing: Nonhydrated[1] eggs only	No. adult females examined
0.22-0.50	0.37	46	15.2	84.8	1,003
.51- .74	0.61	19	13.4	86.6	649
.75- .92	0.84	13	10.9	89.1	384

[1]Classified based on external characteristics of ovaries.
[2]From four to six net haul samples (daytime, 5-11 m) examined each week during 22 March-20 August 1979.

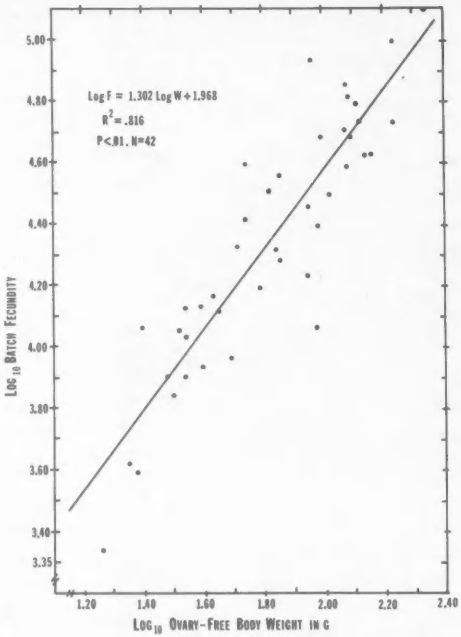

FIGURE 7.—Relation between the common logarithms of batch fecundity and ovary-free body weight of queenfish collected March-August 1979. Regression is the least squares best fit.

Residual Ova

Since not all of the eggs that are ripened and ovulated might be shed, we estimated the numbers of residual, ovulated eggs present in the ovaries of recently spawned, night sample fish. Numbers of residual ova were trivial (Table 7), indicating that females ovulate and shed virtually all of the eggs that undergo hydration.

Annual Egg Production

The spawning season of *S. politus* near San Diego lasts 3-6 mo, being longer for larger females (Table 2). Since batch fecundity is also proportional to female body size, annual egg production of individual fish ranges greatly. We estimate that a 10.5 cm female, spawning once every 7.4 d during May-July, produces about 60,000 eggs, whereas a 25 cm fish that spawns once every 7.4 d over a 6-mo period (March-August) produces nearly 2.3 million eggs. The relatively huge egg production by large *S. politus* thus reflects both greater numbers of spawnings over a longer season and larger batch fecundities.

TABLE 7.—Numbers of residual (ovulated but unspawned) eggs[1] present in spent (Stage 5) ovaries of queenfish. Numbers of residual eggs also expressed as percent of batch fecundity (estimated from standard length).

Item	No. residual ova	Batch fecundity	
		Estimated	Percent
Mean	25	25,500	0.1
Range	2-101	8,100-67,100	0.005- .6

[1]Based on examination of 16 females ($\bar{X}$ = 16.2 cm SL, range 12.1-22.0 cm) collected March-August 1979.

Relative Fecundity

The numbers of eggs produced per unit of body weight, i.e., "relative fecundity" (Nikolskii 1969), is an increasing function of body size in *S. politus* (Figures 4, 8). On a per spawning basis, larger females allocate relatively more energy to egg

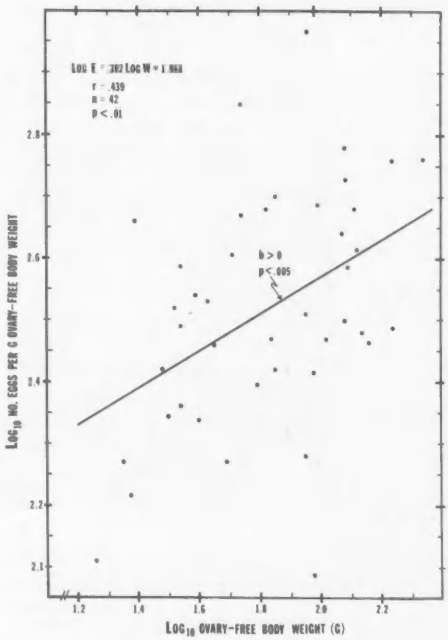

FIGURE 8.—Relation between relative fecundity (as the batch numbers of eggs per gram ovary-free body weight) and ovary-free body weight of queenfish collected March-August 1979. Transformation of raw data to common logarithms provided a tighter correlation (greater R^2) than untransformed data.

production than smaller females. The average 42 g fish produces 287 eggs/g of ovary-free body weight. Values range from an average 218 eggs/g to 494 eggs/g respectively (Figure 8) in a 10.5 cm and a 25 cm fish. Ripening (Stage 2, Table 1) ovaries compose 3.8% (for small fish <13.5 cm) and 4.2% (large fish >13.5 cm) of body weight. Ripe ovaries containing hydrated (Stage 3) oocytes made up an average 7.1% and 8.0% of the body weight of small and large *S. politus*, respectively. The average female produces about 4,570 eggs/g of Stage 3 ovary.

Egg Size

The Gilson's fluid-fixed, hydrated and nonhydrated oocytes of *S. politus* average 540 μm and 400 μm in diameter, respectively, and egg size in general declines as the spawning season progresses (Figure 9). Eggs fixed in Gilson's fluid are 85% the diameter of fresh eggs; thus actual egg size declined from about 685 to 580 μm between March and August 1979. Egg size also varied among different-sized females (Table 8). Throughout the season larger females generally produced larger eggs than did smaller females.

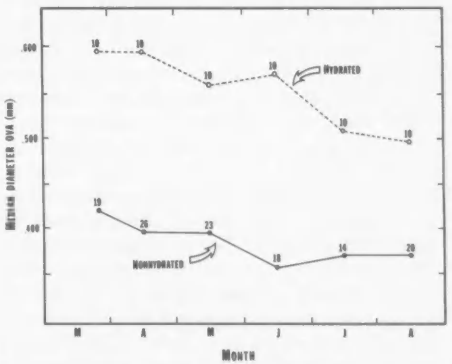

FIGURE 9.—Median diameters (random axis, Gilson's fixed) of the largest size-frequency class of oocytes present in subsampled queenfish of all body sizes collected March-August 1979. Data for fish with Stage 2 and Stage 3 ovaries are plotted separately. Numbers of sample fish are indicated.

TABLE 8.—Results of two-way analysis of variance of the effects of month and female size on the median diameter of the largest oocytes in ripening (Stage 2) ovaries of queenfish. Sample size = 417 fish.

Source of variation	df	*F*	*P*
Main effects	9	7.526	0.001
Month[1]	5	9.783	0.001
Female size[2]	4	3.833	0.005
Two-way interaction:			
Month × size	20	1.597	0.05
Explained	29	3.437	0.001
Residual	387	—	—
Total	416	—	—

[1]Spawning season partitioned into 6 mo: March, April, May, June, July, August 1979.
[2]Females divided into five length classes: 10.6-12.5, 12.6-14.5, 14.6-16.5, 16.6-18.5, >18.5 cm SL.

DISCUSSION

Size at Sexual Maturity

The smallest *S. politus* that contained ripe (Stage 3) eggs were 10.0-10.5 cm SL. At this size females are in their first spring or second summer following birth and average about 13 mo old (DeMartini et al. footnote 4). The onset of egg production by recruit spawners is variable, however; on average only 38% of the females this small contained mature eggs throughout the season, and >10% were generally immature at all lengths <13.5 cm (Table 2). A variable body size at first sexual maturity is a common feature of serial spawners and fishes in general (Nikolskii 1969).

Goldberg (1976) found no histological evidence of sexual maturity in female *S. politus* <14.8 cm SL among those he examined during November 1974-October 1975 from Santa Monica Bay, Calif., about 110 km upcoast of our study area. This might be due to geographic or annual variation in size at maturity, but more likely reflects chance error as only two fish <14.8 cm SL were among those examined (Goldberg[5]).

Body Size and Length of Spawning Season

Duration of the spawning season of repeat-spawning *S. politus* is in general about twice as long as the season for recruit spawners (Table 2). An earlier onset and later cessation of spawning by larger, older individuals is known for other serial spawning fishes of southern California, including northern anchovy (perhaps: see Hunter and Macewicz 1980); Pacific sardine, *Sardinops sagax caeruleus* (Clark 1934); jack mackerel, *Trachurus symmetricus* (Wine and Knaggs 1975); Pacific mackerel, *Scomber japonicus* (Knaggs and Parrish 1973); and California grunion, *Leuresthes*

[5]Stephen R. Goldberg, Department of Biology, Whittier College, Whittier, Calif., pers. commun. August 1978.

tenuis (Clark 1925). A protracted spawning season is generally characteristic of repeat spawners (Nikolskii 1969).

Temporal Patterns of Spawning

The peaks in spawning synchrony among female *S. politus* during the moon's first quarter are likely adaptive for several reasons. Spawning at dusk while the night sky is still fairly dark probably helps conceal adults and planktonic eggs from visual predators. Furthermore, tidal exchanges are minimal during the moon's first quarter (Figure 2B) and the conservation of planktonic eggs and larvae in nearshore areas may be facilitated. Juvenile and adult queenfish inhabit depths <20 m during most of the year (DeMartini and Larson[6]), and most queenfish larvae are found in water <30 m within 4-5 km of shore (Barnett et al.[7]).

Little data exist on the subseasonal spawning patterns of other temperate marine fishes. The data of Clark (1934) suggested monthly spawning peaks for Pacific sardine around times of the full moon. Farris (1963) later showed that no lunar spawning periodicity exists for Pacific sardine and jack mackerel off southern California, although diel and seasonal patterns occur in both species. Northern anchovies spawn between 2200 and 0400 h (Smith 1978, cited in Hunter and Goldberg 1980). A number of north Atlantic fishes have diel spawning periodicities (Simpson 1971). Lunar spawning intervals are known for several littoral fishes that spawn demersal eggs (e.g., California grunion, Clark 1925; mummichog, *Fundulus heteroclitus*, Taylor et al. 1979, Taylor and DiMichele 1980).

Sex Ratio of Spawning Fish

Although the overall adult sex ratio of *S. politus* was only slightly male biased, the male:female sex ratio averaged about 2:1 in groups of fish in which the highest proportion of ready-to-spawn females were present. Hunter and Goldberg (1980) noted the same phenomenon in spawning schools of the northern anchovy and other pelagic spawners. The skewed sex ratio in spawning schools of the queenfish, however, should not bias our estimates of female spawning frequency either for or against spawning females, as may be the case with northern anchovy (Hunter and Goldberg 1980; Hunter and Macewicz 1980), since queenfish were sampled within the entire water column over the total daytime onshore-offshore distribution of the species.

Egg Production and Fish Body Size

The batch fecundity of *S. politus* is proportional to length cubed and is better correlated with weight than with body length, both being general phenomena in fishes (Nikolskii 1969).

The low standing crop ovary weights (2-4% body weight) of *S. politus*, and of multiple-spawning fishes in general (e.g., 6% in the northern anchovy, Smith and Lasker 1978; 4.1-9.0% in the scaled sardine, *Harengula jaguana*, Martinez and Houde 1975), greatly underrepresent total egg production by serial spawners. We estimate that a 25 cm (253 g) *S. politus* with an annual egg production of about 2.2 million eggs (24 batches averaging 90,000 eggs, each egg an average 0.635 mm diameter and 0.134 mg fresh weight) expends the equivalent of 114% of its body weight in eggs in a year. This is not unexpectedly high, since, for example, females of one species of silverside, *Menidia audens*, produce about 6-8 times their body weight in eggs per year (Hubbs 1976). This is, however, considerably more than the seemingly great egg investments made by fishes in which females are single clutched and spawn large, benthic, adhesive eggs (e.g., 20% in the fourhorn sculpin, *Myoxocephalus quadricornis*, Westin 1968; 30% in the red Irish lord, *Hemilepidotus hemilepidotus*, DeMartini and Patten 1979; 34% in the plainfin midshipman, *Porichthys notatus*, DeMartini[8]). Doubtless the poorer survival of small, planktonic eggs and larvae (Ware 1975) necessitates the production of greater numbers of eggs. Partial overlap in the ripening of eggs in successive batches allows greater numbers of eggs of a given size to be produced per unit time, as

[6]E. E. DeMartini and R. J. Larson, Marine Science Institute, Univ. Calif., Santa Barbara, CA 93106, unpubl. data.

[7]Barnett, A. M., A. E. Jahn, P. D. Sertic, and W. Watson. Long term average spatial patterns of ichthyoplankton off San Onofre and their relationship to the position of the SONGS cooling system. A study submitted to the Marine Review Committee of the California Coastal Commission, July 22, 1980. Unpubl. rep., 32 p. Marine Ecological Consultants of Southern California, 533 Stevens Avenue, Suite D-57, Solana Beach, CA 92075.

[8]DeMartini, E. E. Variations in fecundity and growth among geographic populations of the plainfin midshipman, *Porichthys notatus*. Manuscr. in prep. Marine Science Institute, Univ. Calif., Santa Barbara, CA 93106.

space within the female's body cavity must set an upper limit to the numbers of eggs of a given size that can be simultaneously ripened and shed.

Egg production in *S. politus* is not directly proportional to weight, as it is in many marine fishes (Bagenal 1967), but is instead an increasing function of body weight (Figure 8). Relative fecundity thus increases with body size in queenfish, as is also the case for northern anchovy (Hunter and Macewicz 1980) and two other offshore Pacific species, jack mackerel and the gonostomatid *Vinciguerria lucetia* (MacGregor 1976).

Spawning Frequency and Annual Fecundity

The 7-d ovarian cycling frequency of *S. politus* is similar to that of *Engraulis mordax* off southern California, the only other species for which analogous data now exists (Hunter and Goldberg 1980). Having first determined the degeneration rate of ovarian postovulatory follicles in laboratory fish, Hunter and Goldberg (1980) used data on the percent frequency occurrence of 1-d-old ovarian follicles in field sample fish to estimate that *E. mordax* spawns on average once every 6-8 d. Estimates of average spawning interval (5.3 d) based on relative incidence of northern anchovy females bearing hydrated oocytes and new postovulatory follicles were indistinguishable from estimates based on frequency occurrence of day 1 postovulatory follicles (Hunter and Goldberg 1980). Spawning frequency is unrelated to female body size in queenfish and the northern anchovy (Hunter and Macewicz 1980). Incidence of hydration provides accurate estimates of spawning frequency when, as with *E. mordax* and queenfish, an identifiable time of spawning exists, all ripe eggs are shed at this time, and sample fish can be collected accordingly.

Annual egg production is largely dependent on spawning frequency in multiple-spawning fishes. The 6- to 8-d spawning interval of *E. mordax* extrapolated over its 5-mo (January-May) peak spawning season (Lasker and Smith 1977), indicates that an individual northern anchovy ripens and sheds about 20 batches of eggs per year (Hunter and Macewicz 1980). At an average relative fecundity of 421 eggs/g (Hunter and Macewicz 1980), estimated annual egg production of the northern anchovy is over 8,000 eggs/g, or about 14 times greater than previous estimates of annual egg production inferred from standing crop fecundities (606 eggs/g, MacGregor 1968; 556 eggs/g, Norberg[9]). Similarly, our estimates of the annual egg production of *S. politus* range from 12 to 24 times the batch fecundity of recruit spawners (90-d season) and of the largest repeat spawners (180-d season), respectively. These data on the ovarian cycling frequencies of the queenfish and the northern anchovy indicate that prior studies of egg production in multiple-spawning marine fishes have in general underestimated annual egg production by at least an order of magnitude. This seems generally true whether the egg production estimate was based on standing crop fecundity (e.g., Simpson 1951; MacGregor 1957) or standing crop fecundity multiplied by the number of spawnings as inferred from the number of size classes of yolked eggs (e.g., Hickling and Rutenberg 1936; DeSilva 1973; but see Shackley and King 1977). Our queenfish data and Hunter and Goldberg's (1980) data for the northern anchovy illustrate that the spawning frequency (hence annual egg production) of serial-spawning fishes cannot usually be inferred from the number of size-frequency modes of ovarian eggs. It follows that many past estimates of the standing stocks of serial spawners that have inferred female abundance based on egg-larval abundances and female fecundities have greatly overestimated stock sizes.

Production Cycles, Timing of Reproduction, and Egg Size

The seasonality of phyto- and zooplankton production strongly influences the timing of reproduction of temperate marine fishes; in general spawning seasons in the temperate zone are timed so that planktonic offspring are exposed to peak food densities (Cushing 1975). The spawning season of the northern anchovy, a species with many reproductive attributes similar to those of queenfish, coincides with phytoplankton production at the start of the production cycle, yet precedes the disruption of prey patches that occurs due to subsequent upwelling (Lasker 1975, 1978). Queenfish larvae prey on copepodites and adult zooplankters (Barnett et al.[10]), and thus it would

[9]Norberg, R. H. 1975. Investigations on the fecundity of northern anchovy, jack mackerel, and Pacific mackerel. Unpubl. manuscr., 23 p. Calif. Dep. Fish Game, 350 Golden Shore, Long Beach, CA 90802.

[10]Barnett, A. M., P. D. Sertic, and R. Davis. 1980. Data summary of larval fish stomach analysis. A study submitted to the Marine Review Committee of the California Coastal Commission, September 7, 1980. Unpubl. rep., 22 p. Marine Ecological Consultants of Southern California, 533 Stevens Avenue, Suite D-57, Solana Beach, CA 92075.

seem that queenfish reproduction is timed to coincide with peak zooplankton densities later in the production cycle.

Further evidence for the controlling influence of planktonic production on the timing of reproduction by many fishes, including queenfish, comes from subseasonal variations in egg size. Blaxter and Hempel (1963) demonstrated that larval survival is related to hatchling size, which in turn is proportional to egg volume. The egg (hence larval) size of temperate spring-summer spawning species in general declines over the spawning season, whereas size of eggs of autumn-winter spawning species increases over the season (Ware 1975). These changes in egg size coincide with the planktonic production cycle as it affects the kinds, sizes, and quantities of zooplankton prey available for fish larvae. Larval growth and mortality rates (influenced by seasonally changing predator densities and water temperatures as well as densities of planktonic prey) may also elicit adaptive changes in egg size (Ware 1975). A scenario for spring-summer spawners like queenfish might be as follows: At low water temperatures in early spring, growth of fish larvae is slow, relatively few large (adult) zooplankton are available as food for larval fish, and larger hatchlings are better able to temporarily withstand starvation and to capture and ingest large zooplankton. Also, since survival is related to size of larvae (Ware 1975), larger fish larvae have a lower probability of being eaten. As spring becomes summer, water temperatures rise, larvae can grow faster as more zooplankton of a greater array of sizes become available, and it is then adaptive to spawn greater numbers of smaller eggs that subsequently hatch as smaller larvae (Ware 1975). A large number of spring-summer spawners in the temperate zone track the production cycle in this manner (Bagenal 1971). Serial spawning in regions of upwelling appears to be a tropical adaptation to a temperate production cycle of high amplitude that is highly variable in timing (Cushing 1975). Fishes like queenfish spawn on numerous occasions, perhaps so as to "hedge their bet" against unpredictable, and often poor, subseasonal conditions for planktonic propagules. Of course, serial spawning may also be influenced by the fecundity demands necessitated by small adult body size and high adult mortality rates.

We estimate that the spawned eggs of *S. politus* declined from about 685 to 580 μm in diameter over the interval from March to August 1979. This 15% decrease in diameter corresponds to a 39% decrease in volume, or 65% of the difference expressed as a percentage of the smaller volume. This is a reasonable value; for marine fishes with planktonic eggs, the median percentage difference in intraspecific egg volume is just over 100%, with a range from 4.5 to 403% (Bagenal 1971). Assuming that the chemical composition of yolk in queenfish eggs remains constant during the spawning season, the calorific value of individual eggs declined by about 39%. Since the relation between batch fecundity and female body size is constant throughout the spawning season (Figure 6), queenfish appear to allocate less energy to egg production later in the season by producing smaller eggs. *Engraulis mordax* likewise produces smaller (Smith and Lasker 1978) and perhaps fewer (Hunter[11]) eggs later in its spawning season. The availability of food for adults as well as larvae appears to determine the timing and intensity of spawning by northern anchovy (Hunter and Goldberg 1980) as well as queenfish and perhaps also influences egg size in these fishes.

SUMMARY

The queenfish is a serial spawner with a protracted spawning season. Spawning frequency, although generally asynchronous among females, can be estimated from the incidence of fish with hydrated eggs and averages about once per week for females of all adult sizes. Duration of the spawning season, however, is proportional to female body size, ranging from 3 mo (April-June) in recruit spawners (10.0-10.5 cm SL) to 6 mo (March-August) in repeat spawners (>13.5 cm). Larger females begin spawning earlier in the year and continue spawning after the smallest fish have ceased. Recruit spawners and the largest repeat spawners thus produce about 12 to 24 batches of eggs during their respective spawning seasons.

Batch fecundity is proportional to female body size and is better correlated with weight than with length of female. Batch fecundity ranges from about 5,000 eggs in 10.5 cm SL recruit spawners to about 90,000 eggs in the largest (25 cm) repeat spawners. The average (14 cm) fish produces about 12,000-13,000 eggs per batch. Almost all hydrated eggs are liberated at the time of spawning, which

[11]J. Roe Hunter, Southwest Fisheries Center, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. August 1980.

occurs at dusk and has monthly peaks in intensity during the week of the moon's first quarter.

Annual egg production ranges from about 60,000 eggs to over 2.2 million eggs in the smallest recruit spawner and the largest repeat spawner, respectively. The average female produces about 300,000 eggs in a year. These estimates of annual egg production are an order of magnitude greater than usually would be inferred based on oocyte size class frequencies.

Relative fecundity of the queenfish is an increasing function of body size. Larger females produce larger eggs, and females of all adult sizes produce larger eggs earlier in the season.

As reflected by the general nature of its protracted, serial spawning activities and by the timing of subseasonal variations in its egg size and in the female size-to-egg size and egg number relationships, the queenfish closely resembles many or most small, planktonic spawners of warm temperate regions. We suggest that the reproductive dynamics of the queenfish typify the suite of reproductive adaptations characteristic of small, short-lived fishes that must cope with irregular (unpredictable) subseasonal variations in planktonic productivity.

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LITERATURE CITED

BAGENAL, T. B.
1967. A short review of fish fecundity. *In* S. D. Gerking (editor), The biological basis of freshwater fish production, p. 89-111. Blackwell Sci. Publ., Oxf., Engl.
1971. The interrelation of the size of fish eggs, the date of spawning and the production cycle. J. Fish Biol. 3:207-219.

BAGENAL, T. B., AND E. BRAUM.
1971. Eggs and early life history. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, p. 166-198. IBP (Int. Biol. Programme) Handb. 3.

BLAXTER, J. H. S., AND G. HEMPEL.
1963. The influence of egg size on herring larvae (*Clupea harengus* L.). J. Cons. 28:211-240.

CLARK, F. N.
1925. The life history of *Leuresthes tenuis*, an atherine fish with tide controlled spawning habits. Calif. Dep. Fish Game, Fish Bull. 10, 51 p.
1930. Size at first maturity of the white sea bass (*Cynoscion nobilis*). Calif. Fish Game 16:319-323.
1934. Maturity of the California sardine (*Sardina caerulea*), determined by ova diameter measurements. Calif. Dep. Fish Game, Fish Bull. 42, 49 p.

CONOVER, W. J.
1971. Practical nonparametric statistics. Wiley, N.Y., 462 p.

CUSHING, D. H.
1975. Marine ecology and fisheries. Camb. Univ. Press, N.Y., 278 p.

DeMARTINI, E. E., AND B. G. PATTEN.
1979. Egg guarding and reproductive biology of the red Irish lord, *Hemilepidotus hemilepidotus* (Tilesius). Syesis 12:41-55.

DeSILVA, S. S.
1973. Aspects of the reproductive biology of the sprat, *Sprattus sprattus* (L.) in inshore waters of the west coast of Scotland. J. Fish Biol. 5:689-705.

FARRIS, D. A.
1963. Reproductive periodicity in the sardine (*Sardinops caerulea*) and the jack mackerel (*Trachurus symmetricus*) on the Pacific coast of North America. Copeia 1963: 182-184.

FEDER, H. M., C. L. TURNER, AND C. LIMBAUGH.
1974. Observations on fishes associated with kelp beds in southern California. Calif. Dep. Fish Game, Fish Bull. 160, 144 p.

FITCH, J. E., AND R. J. LAVENBERG.
1971. Marine food and game fishes of California. Univ. Calif. Press, Berkeley, 179 p.
1975. Tidepool and nearshore fishes of California. Univ. Calif. Press, Berkeley, 156 p.

FREY, H. W.
1971. California's living marine resources and their utilization. Calif. Dep. Fish Game, Mar. Res. Agency, 148 p.

GOLDBERG, S. R.
1976. Seasonal spawning cycles of the sciaenid fishes *Genyonemus lineatus* and *Seriphus politus*. Fish. Bull., U.S. 74:983-984.

HICKLING, C. F., AND E. RUTENBERG.
1936. The ovary as an indicator of the spawning period in fishes. J. Mar. Biol. Assoc. U.K. 21:311-316.

HIGHAM, J. R., AND W. R. NICHOLSON.
1964. Sexual maturation and spawning of Atlantic menhaden. Fish. Bull., U.S. 63:255-271.

HTUN-HAN, M.
1978. The reproductive biology of the dab *Limanda limanda* (L.) in the North Sea: seasonal changes in the ovary. J. Fish Biol. 13:351-359.

HUBBS, C.
1976. The diel reproductive pattern and fecundity of *Menidia audens*. Copeia 1976:386-388.

HUNTER, J. R., AND S. R. GOLDBERG.
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77: 641-652.

HUNTER, J. R., AND B. J. MACEWICZ.
1980. Sexual maturity, batch fecundity, spawning frequency, and temporal pattern of spawning for the northern anchovy, *Engraulis mordax*, during the 1979 spawning season. Calif. Coop. Oceanic Fish. Invest. Rep. 21:139-149.

KNAGGS, E. H., AND R. H. PARRISH.
1973. Maturation and growth of Pacific mackerel *Scomber japonicus* Houttuyn. Calif. Dep. Fish Game, Mar. Res. Tech. Rep. 3, 19 p.

LASKER, R.
1975. Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73:453-462.
1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 173:212-230.

LASKER, R., AND P. E. SMITH.
1977. Estimation of the effects of environmental variations on the eggs and larvae of the northern anchovy. Calif. Coop. Oceanic Fish. Invest. Rep. 19:128-137.

LIMBAUGH, C.
1961. Life history and ecologic notes on the black croaker. Calif. Fish Game 47:163-174.

MACER, C. T.
1974. The reproductive biology of the horse mackerel *Trachurus trachurus* (L.) in the North Sea and English Channel. J. Fish Biol. 6:415-438.

MACGREGOR, J. S.
1957. Fecundity of Pacific sardine (*Sardinops caerulea*). U.S. Fish Wildl. Serv., Fish. Bull. 57:427-449.
1968. Fecundity of the northern anchovy, *Engraulis mordax* Girard. Calif. Fish Game 54:281-288.
1976. Ovarian development and fecundity of five species of California current fishes. Calif. Coop. Oceanic Fish. Invest. Rep. 18:181-188.

MARTINEZ, S., AND E. D. HOUDE.
1975. Fecundity, sexual maturation, and spawning of scaled sardine (*Harengula jaguana* Poey). Bull. Mar. Sci. 25:35-45.

MILLER, D. J., AND R. N. LEA.
1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 157, 235 p.

MOSER, H. G.
1967. Reproduction and development of *Sebastodes paucispinis* and comparison with other rockfishes off southern California. Copeia 1967:773-797.

NIKOLSKII, G. V.
1969. Theory of fish population dynamics as the biological background for rational exploitation and management of fishery resources. Oliver & Boyd, Edinb., 323 p.

SHACKLEY, S. E., AND P. E. KING.
1977. The reproductive cycle and its control; frequency of spawning and fecundity in *Blennius pholis* L. J. Exp. Mar. Biol. Ecol. 30:73-83.

SIEGEL, S.
1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, N.Y., 312 p.

SIMPSON, A. C.
1951. The fecundity of the plaice. Fish. Invest. Minist. Agric. Fish. Food (G.B.) Lond., Ser. II, 17(5), 27 p.
1971. Diel spawning behaviour in populations of plaice, dab, sprat and pilchard. J. Cons. 34:58-64.

SKOGSBERG, T.
1939. The fishes of the family Sciaenidae (croakers) of California. Calif. Div. Fish Game, Fish Bull. 54:1-62.

SMITH, P. E., AND R. LASKER.
1978. Position of larval fish in an ecosystem. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 173:77-84.

TAYLOR, M. H., AND L. DIMICHELE.
1980. Ovarian changes during the lunar spawning cycle of *Fundulus heteroclitus*. Copeia 1980:118-125.

TAYLOR, M. H., G. J. LEACH, L. DIMICHELE, W. M. LEVITAN, AND W. F. JACOB.
1979. Lunar spawning cycle in the mummichog, *Fundulus heteroclitus* (Pisces: Cyprinodontidae). Copeia 1979: 291-297.

WARE, D. M.
1975. Relation between egg size, growth, and natural mortality of larval fish. J. Fish. Res. Board Can. 32: 2503-2512.

WESTIN, L.
1968. The fertility of fourhorn sculpin, *Myoxocephalus quadricornis* (L). Inst. Freshwater Res. Drottningholm Rep. 48:67-70.

WINE, V. L., AND E. H. KNAGGS.
1975. Maturation and growth of jack mackerel, *Trachurus symmetricus*. Calif. Dep. Fish Game, Mar. Res. Tech. Rep. 32:1-25.

YAMAMOTO, K., AND F. YAMAZAKI.
1961. Rhythm of development in the oocyte of the gold-fish, *Carassius auratus*. Bull. Fac. Fish. Hokkaido Univ. 12:93-110.

YAMAMOTO, K., AND H. YOSHIOKA.
1964. Rhythm of development in the oocyte of the medaka, *Oryzias latipes*. Bull. Fac. Fish. Hokkaido Univ. 15:5-19.

YOUNG, P. H.
1963. The kelp bass (*Paralabrax clathratus*) and its fishery, 1947-1958. Calif. Dep. Fish Game, Fish Bull. 122, 67 p.

ZWEIFEL, J. R., AND P. E. SMITH.
In press. A time series of anchovy embryonic and larval mortality estimates with method for confidence limits on the estimates of abundance of all sizes and on the mortality rate. *In* R. Lasker and K. Sherman (editors), The early life history of fish. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 177.

NOTES

SEASONAL SPAWNING CYCLE OF THE BLACK CROAKER, *CHEILOTREMA SATURNUM* (SCIAENIDAE)

Detailed information is lacking on the spawning cycle of the black croaker, *Cheilotrema saturnum*. Previous works (Eigenmann 1892; Skogsberg 1939; Limbaugh 1961; Fitch and Lavenberg 1975) have indicated spawning occurs in spring and summer. This report describes the histological changes occurring in the spawning cycle. Comparisons are made with the spawning cycles of two other sciaenid fishes (*Genyonemus lineatus* and *Seriphus politus*) which were studied by Goldberg (1976). *Cheilotrema saturnum* ranges from Magdalena Bay, Baja California, to Point Conception, Calif. (Miller and Lea 1976).

Methods

A total of 154 mature female *C. saturnum* were examined from collections made in January, March, July, September 1977 and 1978. Specimens were collected during heat treatment processes at the Scattergood Steam Plant (City of Los Angeles, Department of Water and Power, LADWP), El Segundo (lat. 33°50′ N, long. 118°30′ W), Los Angeles County, Calif. Steam generating plants periodically reverse the flow of cooling water in their intake and discharge pipes and raise the temperature to a level that will kill off entrapped organisms. Immediately after collection, fish were slit along the abdomen and placed in 10% Formalin.[1] Ovaries were embedded in paraffin; sections were cut at 8 μm and stained with iron hematoxylin. Body and ovary weights were measured on a torsion balance to the nearest 0.01 g. Standard lengths (SL) were measured to the nearest millimeter. Gonosomatic indices (GSI = ovary weight/fish weight × 100) were calculated from measurements made after preservation.

Results and Discussion

Ovaries were classified histologically into four stages (Table 1). Stage 1 (regressed or regressing ovary): the nonspawning condition consists principally of primary oocytes (<100 μm in diameter). Stage 2 (previtellogenic): slightly enlarged vacuolated oocytes (100-200 μm in diameter) predominate prior to onset of yolk deposition. Stage 3 (vitellogenic): yolk deposition in progress. Stage 4 (spawning): mature (ripe) oocytes (>300 μm) predominate.

Ovaries were regressed (Stage 1) during autumn and winter (Table 1, Figure 1). GSI values began to increase during winter and Stage 2 oocytes became common. In late spring enlarging follicles undergoing yolk deposition (vitellogenesis) were

TABLE 1. Monthly distribution of standard lengths and stages in *Cheilotrema saturnum* spawning cycle, January 1977-November 1978.

Month	N	Range (mm)	Stage 1 (%)	Stage 2 (%)	Stage 3 (%)	Stage 4 (%)
Jan.	6	160-240	100	0	0	0
Mar.	16	181-296	87	13	0	0
May	7	167-292	43	29	14	14
July	15	194-280	0	0	7	93
Sept.	6	160-232	83	0	0	17
Nov.	8	171-267	100	0	0	0
Jan.	16	166-283	100	0	0	0
Mar.	14	172-260	50	50	0	0
May	12	168-255	0	25	8	67
July	29	161-262	0	0	10	90
Sept.	11	165-231	64	9	0	27
Nov.	14	167-265	100	0	0	0

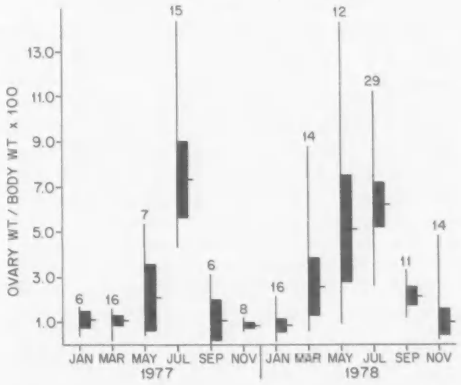

FIGURE 1.—Seasonal gonosomatic indices for *Cheilotrema saturnum*. Vertical line = range; horizontal line = mean; rectangle = 95% confidence interval and sample size above each month.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

present (Stage 3). Other fish examined at this time were in spawning condition (Stage 4) and contained ovaries with mature yolk-filled oocytes. The peak of spawning activity occurred in midsummer (July). Most spawning was completed by September as GSI values dropped and numbers of spawning females were fewer (Table 1). Atretic oocytes were common in September near the close of the spawning period when oocytes that failed to complete yolk deposition underwent resorption. They were observed in 67% of my combined 1977-78 September samples.

Rather than maturing and spawning one mode (size class) of eggs at a time, it seems that females reach spawning condition and then release batches of mature eggs throughout the spawning season. This is likely, as no summer females were observed with ovaries in postspawning (partly spent or spent) condition. Instead, *C. saturnum* oocyte development appears to be a continuous process during the spawning season, as ovaries at all times contained maturing and large numbers of mature oocytes. I have previously observed this pattern (Goldberg 1976) in *G. lineatus* and *S. politus*.

Postovulatory follicles (transitory remnants of the follicle wall from recently ovulated eggs) were seen in only 2% of my combined 1977-78 July samples. Ovaries containing these structures were in spawning condition. This low percentage is not unexpected in view of their rapid degeneration in teleost fishes (Yamamoto and Yoshioka 1964; Hunter and Goldberg 1980).

The spawning cycle of *C. saturnum* is similar to that of *S. politus*, namely, April-August (Goldberg 1976). Spawning in *G. lineatus* occurs November-April (Goldberg 1976) and is thus distinctly different from that of *C. saturnum* and *S. politus*. According to Feder et al. (1974) three other California sciaenids (*Atractoscion nobilis*, *Menticirrhus undulatus*, and *Roncador stearnsii*) are also summer spawners.

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Literature Cited

EIGENMANN, C. H.
1892. The fishes of San Diego, California. U.S. Natl. Mus. Proc. 15:123-178.

FEDER, H. M., C. H. TURNER, AND C. LIMBAUGH.
1974. Observations on fishes associated with kelp beds in southern California. Calif. Dep. Fish Game, Fish Bull. 160, 144 p.

FITCH, J. E., AND R. J. LAVENBERG.
1975. Tidepool and nearshore fishes of California. Univ. Calif. Press, Berkeley, 156 p.

GOLDBERG, S. R.
1976. Seasonal spawning cycles of the sciaenid fishes *Genyonemus lineatus* and *Seriphus politus*. Fish. Bull., U.S. 74:983-984.

HUNTER, J. R., AND S. R. GOLDBERG.
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77: 641-652.

LIMBAUGH, C.
1961. Life-history and ecologic notes on the black croaker. Calif. Fish Game 47:163-174.

MILLER, D. J., AND R. N. LEA.
1976. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 157, 249 p.

SKOGSBERG, T.
1939. The fishes of the family Sciaenidae (croakers) of California. Calif. Dep. Fish Game, Fish Bull. 54, 62 p.

YAMAMOTO, K., AND H. YOSHIOKA.
1964. Rhythm of development in the oocyte of the medaka, *Oryzias latipes*. Bull. Fac. Fish. Hokkaido Univ. 15:5-19.

STEPHEN R. GOLDBERG

Department of Biology
Whittier College
Whittier, CA 90608

POPULATION GROWTH AND CENSUSES OF THE NORTHERN ELEPHANT SEAL, *MIROUNGA ANGUSTIROSTRIS*, ON THE CALIFORNIA CHANNEL ISLANDS, 1958-78

The northern elephant seal, *Mirounga angustirostris*, has received considerable attention because of its dramatic recovery from near extinction in the late 19th century. Bartholomew and Hubbs (1960) reviewed the chronicle of the species from 1818 to 1960 and estimated the total population over its then known range at about 13,000 animals. Since 1960, a number of investigators have reported on the reestablishment of elephant seals on progressively northern islands and on the size of its breeding populations. Such information is now available for the islands of the Pacific coast of North America from Isla Natividad, Baja California,

northward to the Farallon Islands, Calif. (Bartholomew and Boolootian 1960; Radford et al. 1965; Rice et al. 1965; Carlisle and Aplin 1966, 1971; Carlisle 1973; Frey and Aplin 1970; Odell 1971, 1972, 1974; Le Boeuf et al. 1974; Le Boeuf and Mate 1978; Bonnell et al.[1]). By 1978 the total population was believed to have increased to an astounding 63,967 animals (Bonnell et al. footnote 1).

The northern elephant seal breeding population can be geographically divided into three subpopulations by centers of distribution (Figure 1): Baja California; California Channel Islands, including Islas Los Coronados, Baja California; and Central California (Gogan[2]).

One can trace a rapid increase in size of the California Channel Island subpopulation (hereinafter called the subpopulation) over the last nearly three decades. Rett (1952) reported seeing a single female on San Miguel Island in 1925. Bartholomew and Hubbs (1960) estimated that by 1957 the subpopulation contained 600 individuals. Births were first observed on San Miguel Island in 1958 and on San Nicolas Island in 1959, by which time the total subpopulation included an estimated 683 animals (Bartholomew and Boolootian 1960). By 1964, there were reportedly 2,158 elephant seals on three islands during the winter breeding season[3]: San Miguel (1,922), San Nicolas (197), and Santa Barbara (39) (Odell 1971). Based on cumulative data obtained during 4 yr of research, Bonnell et al. (footnote 1) estimated that by 1978 there were approximately 28,316 elephant seals in the subpopulation.

In this paper we report on counts of northern elephant seals conducted on all the California Channel Islands, including Islas Los Coronados, in February 1972. Using estimated pup production figures from this and other published censuses for the years 1958-78, we then assess rates of growth for each island within the subpopulation and for the subpopulation as a whole. The relative contributions of each island to the subpopulation total are also presented.

FIGURE 1.—Subdivision of the islands of California and northwestern Baja California into groups, corresponding with designated subpopulations of northern elephant seals (modified from Le Boeuf 1977; Gogan text footnote 2; Bonnell et al. text footnote 1).

Materials and Methods

On 8 February 1972, observers surveyed beaches of all California Channel Islands (except Islas Los Coronados) from U.S. Navy helicopters flying at an altitude of 150 m (500 ft) and a speed of 90 kn, taking large format (9 in × 9 in), near-vertical aerial photographs of all elephant seals seen. Counts of elephant seals were made from glossy black and white prints arranged into mosaics and handled in the manner described by Odell (1971). When possible, animals were differentiated as adult males, adult females, and pups. Counts on the Islas Los Coronados were made from the beach by swimmers dispatched from small boats anchored near shore. All counts represented minimum numbers in the population because an unquantified portion is always at sea (Le Boeuf 1972).

[1]Bonnell, M. L., B. J. Le Boeuf, M. O. Pierson, D. H. Dettman, G. D. Farrens, C. B. Heath, R. F. Gantt, and D. J. Larsen. 1980. Summary of marine mammal and seabird surveys of the Southern California Bight area 1975-1978. Vol. 3-Investigators' Reports, Part 1 - Pinnipeds of the Southern California Bight, 535 p. Univ. Calif., Santa Cruz, Calif., Final Report to the Bureau of Land Management, under Contract AA550-CT7-367.

[2]Gogan, P. J. P. 1977. A review of the population ecology of the northern elephant seal (*Mirounga angustirostris*). Processed Rep., 68 p. Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Boulevard E., Seattle, WA 98112.

[3]For descriptions of seasonal fluctuations in numbers of northern elephant seals on land see Le Boeuf (1972) and Odell (1972).

Counts of suckling and weaned elephant seal pups from this and other censuses between 1958 and 1978 were assembled and compared. Because most pups remain on land until late February (Le Boeuf et al. 1972; Reiter et al. 1978) and are highly visible, they are easily counted during February surveys. We believe, therefore, that pup production estimates are the most accurate available means of assessing, from census data, trends in population numbers of elephant seals.

Total pup production estimates were extrapolated from pup counts (Odell 1974) by correcting for date of census using the equation:

$$\frac{Pi}{f} = Pt$$

where Pi = pups counted at time of census,
f = fraction of maximum pup numbers counted at time of census (Odell 1974, fig. 6),
Pt = estimated total number of pups born that year.

This calculation assumes that the temporal pattern of births on all Channel Island rookeries is not significantly different from that reported for San Nicolas Island (Odell 1974). Corrections are not made for neonatal mortality since rookery specific data are not available.

Three indices of population growth were calculated from both pup counts and estimated total pup production: RC = the relative contributions of each island expressed as a percentage of the total pup counts for each census year; $I\bar{r}$ = the estimated average annual rate of increase for each island; and $S\bar{r}$ = the estimated average annual rates of increase for the entire subpopulation. The average rates of increase ($\bar{r}$) were derived from the formula, $N_t = N_0 e^{\bar{r}t}$ where $\bar{r}$ carries no implication that the rate of increase is constant over the time interval, that the age distribution is constant, or that the resources are in superabundance (Caughley 1977). Thus, $\bar{r}$ can be used as a standardized means of comparing the rates of population increase from one census year to the next.

Results and Discussion

Results of the 1972 census are shown for each island, according to elephant seal age/sex class, in Table 1. All 1972 breeding season counts were greater than similar counts reported previously by Odell (1971) and Le Boeuf et al. (1975).

TABLE 1.—1972 breeding season census of northern elephant seals taken 8 February on the California Channel Islands, including Islas Los Coronados (see Figure 1). Unless otherwise noted, counts were made from aerial photographs.

Island	Adult males	Adult females	Total adults	Pups	Total animals
San Miguel	497	1,410	1,907	1,902	3,809
San Nicolas	103	305	408	399	807
Santa Barbara	4	39	43	26	69
Los Coronados[1]	6	27	33	6	39
San Clemente	0	20	20	0	20

[1]Land-based census.

Pup counts and the computed values they support for the indices RC, $I\bar{r}$, and $S\bar{r}$, are shown in Table 2 for the years between 1958 (San Miguel Island), 1959 (San Nicolas Island), or 1964 (Santa Barbara Island and Islas Los Coronados) and 1978. There was little difference in the indices that were calculated from actual pup counts and those from total pup production estimates (Table 2).

Although the California Channel Island elephant seal subpopulation as a whole and each of its component island colonies have continued to grow over the last 16-22 yr, the rates of increase and individual island contributions to the subpopulation have varied (Table 2).

Relative Island Contribution (RC)

In general the ranked island contributions relative to the total subpopulation pup counts from highest to lowest have been: San Miguel, San Nicolas, Santa Barbara, and Islas Los Coronados (Table 2). Consistent with that trend, in 1958-59 San Miguel Island contributed 55.9% and San Nicolas Island 44.1% of the known subpopulation. But by 1964, the San Miguel Island population had grown so fast that its pup population was an estimated 10 times greater than the San Nicolas Island population, accounting for 90% of the entire subpopulation. During the subsequent period, 1964 to 1972, the RC values decreased for San Miguel Island (81.5), increased for San Nicolas Island (17.1), and remained about the same for Santa Barbara Island (1.1). From 1972 to 1978 there was generally little change in the RC values for all islands.

Increases in numbers of elephant seals and RC values can reasonably be expected on San Miguel and San Nicolas Islands where there are remaining unused beaches suitable for breeding rookeries (Le Boeuf and Bonnell 1980). However,

TABLE 2.—Counts of northern elephant seal pups in the California Channel Islands subpopulation, including Islas Los Coronados (see Figure 1). Unless otherwise noted, counts were obtained from aerial photographs. Also presented are relative contributions by each island (RC) expressed as a percentage of the total pup count and average yearly rates of increase in pup production for each island ($I\bar{r}$) and for the Channel Islands subpopulation ($S\bar{r}$).

Island	Census date	Source		Pup counts		RC		$I\bar{r}$		$S\bar{r}$	
San Miguel	14 Feb. 1958[1]	Bartholomew and Boolootian 1960		[2]80	(81)	[3]62.5	(55.9)				
San Nicolas	23 Jan. 1959[1]	Bartholomew and Boolootian 1960		48	(64)	37.5	(44.1)				
Santa Barbara	Not censused										
Los Coronados	Not censused										
			Total	128	(145)						
San Miguel	9 Feb. 1964	Odell 1971		796	(812)	90.0	(89.8)	[3]0.383	(0.384)		
San Nicolas	9 Feb. 1964			78	(80)	8.8	(8.9)	.081	(.037)		
Santa Barbara	9 Feb. 1964			12	(12)	1.2	(1.3)			[3]0.322	(0.305)
Los Coronados	12 Jan. 1964	Le Boeuf et al. 1975		0							
			Total	886	(904)						
San Miguel	8 Feb. 1972	This study		1,902	(1,941)	81.5	(81.5)	.109	(.109)		
San Nicolas	8 Feb. 1972			399	(407)	17.1	(17.1)	.204	(.203)		
Santa Barbara	8 Feb. 1972			26	(27)	1.1	(1.1)	.097	(.101)		
Los Coronados	8 Feb. 1972[4]			6	(6)	.3	(.3)				
			Total	2,333	(2,381)					.121	(.121)
San Miguel	27 Jan. 1978	Bonnell et al. text footnote 1		4,512	(5,013)	84.6	(84.2)	.144	(.158)		
San Nicolas	29 Jan. 1978			782	(850)	14.7	(14.3)	.112	(.123)		
Santa Barbara	29 Jan. 1978			37	(40)	.7	(.7)	.059	(.066)		
Los Coronados	29 Jan. 1978				[5](45)		(.8)		(.336)	.138	(.153)
			Total	5,331	(5,948)						

[1]The 1958 and 1959 census data averaged and treated as a single census year.
[2]Actual counts, followed in parentheses by total pup production estimates which were corrected for times when less than maximum pup numbers can be counted.
[3]Values calculated from actual pup counts, followed in parentheses by values calculated from total pup production estimates.
[4]Land based census.
[5]Only estimated value reported (Bonnell et al. text footnote 1).

the fact that there is apparently little suitable space available for new elephant seal rookeries on Santa Barbara Island and Islas Los Coronados (Le Boeuf et al. 1975; Bonnell et al. footnote 1) suggests that the numbers on those islands have stabilized and that there will be a concommitant decline in their RC values in future years.

Estimated Average Annual Rate of Increase by Island ($I\bar{r}$)

The $I\bar{r}$ values peaked between 1958 and 1964 on San Miguel Island and between 1964 and 1972 on San Nicolas and Santa Barbara Islands. Data presented suggest that numbers on Islas Los Coronados probably increased most rapidly between 1972 and 1978. This suggestion is supported by results of a more detailed study of those islands which provide data for intermediate years during this period (Le Boeuf et al. 1975).

Generally for each island, periods of high annual increase in population have been followed by periods of decreasing $I\bar{r}$ values. Such trends in reduction of growth rate can be expected to continue until such time as each island's elephant seal numbers reach stability, a pattern of population growth characteristic of other large marine and terrestial mammals (Fowler[4]). The increase from 1972 to 1978 on San Miguel Island is not surprising for an island where space does not appear to be a limiting factor, and similar increases might yet occur on the other islands where suitable breeding space is available. High rates of increase might also occur on new rookeries as northern elephant seals begin to colonize such areas as San Clemente Island and the mainland (Le Boeuf and Panken 1977; Le Boeuf and Mate 1978). But it is highly unlikely that any of the presently colonized California Channel Islands will ever experience growth periods that will exceed the largest $I\bar{r}$ values presented in Table 2.

Estimated Average Annual Rate of Increase in the Subpopulation ($S\bar{r}$)

The most rapid growth in the Channel Island subpopulation as a whole apparently occurred between 1958 and 1964. During this period, $S\bar{r}$ values reached 0.384 then dropped to 0.121 for 1964-72 and 0.153 for 1972-78. The extremely high rate of increase observed from 1958 to 1964 was proba-

[4]Fowler, C. W. 1978. Appendix C. Non-linearity in population dynamics with special reference to large mammals. *In* C. W. Fowler, W. T. Bunderson, M. B. Cherry, R. J. Ryel, and B. B. Steel. Comparative population dynamics of large mammals: a search of management criteria, p. 174-220. Report to U.S. Marine Mammal Commission, Wash., D.C. (Available Natl. Tech. Inf. Serv., Springfield, VA 22161 as PB80-178627.)

bly the result of recruitment both from the Baja subpopulation and from within the California Channel Island subpopulation (Chapman in press; Gogan footnote 2).

Although the Channel Islands subpopulation as a whole may continue to grow, it is likely that future $S\bar{r}$ values will eventually follow the decreasing trend towards stability which was described above for $I\bar{r}$ values (Fowler footnote 4).

Other California Channel Islands

Breeding colonies were not observed on any of the remaining Channel Islands during the 1972 censuses. The small numbers of animals seen on San Clemente Island included no pups, although there is a more recent indication that breeding/pupping sometimes occurs there. A single female with a pup was observed on San Clemente Island in January 1977 (Le Boeuf and Mate 1978). However, no pups were observed there during the 1978 breeding season surveys from land by Cohen.[5]

Anacapa Island may not offer suitable habitat for elephant seals because of its high cliffs and rocky coastline. The beaches on San Clemente Island are near a naval shore bombardment range and frequent bombing may have prevented the animals from establishing a breeding colony there. However, reasons for the absence of elephant seals on Santa Cruz, Santa Rosa, and Catalina Islands, all of which have some beaches which appear suitable, are not known, although human disturbance may be an important factor (Kenyon[6]).

Acknowledgments

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[5]Robert H. Cohen, Naval Ocean Systems Center, San Diego, CA 92152, pers. commun. March 1978.

[6]Kenyon, K. W. 1973. Human disturbance of marine birds and marine mammals in wilderness areas of Baja California, Mexico, 10-17 February 1973. Unpubl. manuscr., 16 p. U.S. Dep. Inter., Bur. Sport Fish. Wildl., Div. Wildl. Res., Mar. Mammal Substation, Seattle, Wash. (Available Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.)

Literature Cited

BARTHOLOMEW, G. A., AND R. A. BOOLOOTIAN.
1960. Numbers and population structure of the pinnipeds on the California Channel Islands. J. Mammal. 41:366-375.

BARTHOLOMEW, G. A., AND C. L. HUBBS.
1960. Population growth and seasonal movements of the northern elephant seal, *Mirounga angustirostris*. [Fr. abstr. and resume.] Mammalia 24:313-324.

CARLISLE, J. G., JR.
1973. The census of northern elephant seals on San Miguel Island, 1965-1973. Calif. Fish Game 59:311-313.

CARLISLE, J. G., JR., AND J. A. ALPIN.
1966. Sea lion census for 1965 including counts of other California pinnipeds. Calif. Fish Game 52:119-120.
1971. Sea lion census for 1970, including counts of other California pinnipeds. Calif. Fish Game 57:124-125.

CAUGHLEY, G.
1977. Analysis of vertebrate populations. Wiley, N.Y., 234 p.

CHAPMAN, D. G.
In press. Evaluation of marine mammal population models. *In* C. W. Fowler and T. D. Smith (editors), Dynamics of large mammal populations. Wiley, N.Y.

FREY, H. W., AND J. A. ALPIN.
1970. Sea lion census for 1969, including counts of other California pinnipeds. Calif. Fish Game 56:130-133.

LE BOEUF, B. J.
1972. Sexual behavior in the northern elephant seal, *Mirounga angustirostris*. Behaviour 41:1-26.
1977. Back from extation? Pac. Discovery 30(5):1-9.

LE BOEUF, B. J., D. G. AINLEY, AND T. J. LEWIS.
1974. Elephant seals of the Farallons: population structure of an incipient breeding colony. J. Mammal. 55:370-385.

LE BOEUF, B. J., AND M. BONNELL.
1980. Pinnipeds of the California Islands: abundance and distribution. *In* D. M. Power (editor), The California Islands: proceedings of a multidisciplinary symposium, p. 475-493. Santa Barbara, California, Santa Barbara Museum of Natural History.

LE BOEUF, B. J., D. A. COUNTRYMAN, AND C. L. HUBBS.
1975. Records of elephant seals, *Mirounga angustirostris*, on Los Coronados Islands, Baja California, Mexico, with recent analyses of the breeding population. Trans. San Diego Soc. Nat. Hist. 18:1-7.

LE BOEUF, B. J., AND B. R. MATE.
1978. Elephant seals colonize additional Mexican and California islands. J. Mammal. 59:621-622.

LE BOEUF, B. J., AND K. J. PANKEN.
1977. Elephant seals breeding on the mainland in California. Proc. Calif. Acad. Sci. 41:267-280.

LE BOEUF, B. J., R. J. WHITING, AND R. F. GANTT.
1972. Perinatal behavior of northern elephant seal females and their young. Behaviour 43:121-156.

ODELL, D. K.
1971. Censuses of pinnipeds breeding on the California Channel Islands. J. Mammal. 52:187-190.
1972. Studies on the biology of the California sea lion and the northern elephant seal on San Nicolas Island, California. Ph.D. Thesis, Univ. California, Los Ang., 168 p.
1974. Seasonal occurrence of the northern elephant seal, *Mirounga angustirostris*, on San Nicolas Island, California. J. Mammal. 55:81-95.

RADFORD, K. W., R. T. ORR, AND C. L. HUBBS.
1965. Reestablishment of the northern elephant seal (*Mirounga angustirostris*) off Central California. Proc. Calif. Acad. Sci. 31:601-612.
REITER, J., N. L. STINSON, AND B. J. LE BOEUF.
1978. Northern elephant seal development: The transition from weaning to nutritional dependance. Behav. Ecol. Sociobiol. 3:337-367.
RETT, E. Z.
1952. The northern elephant seal on San Miguel Island, California. J. Mammal. 33:109.
RICE, D. W., K. W. KENYON, AND L. B. LLUCH.
1965. Pinniped populations at Islas Guadalupe, San Benitos, and Cedros, Baja California, in 1965. Trans. San Diego Soc. Nat. Hist. 14:73-84.

GEORGE A. ANTONELIS, JR.

National Marine Mammal Laboratory
National Marine Fisheries Service, NOAA
7600 Sand Point Way NE.
Seattle, WA 98115

STEPHEN LEATHERWOOD

Hubbs-Sea World Research Institute
1700 South Shores Road
San Diego, CA 92109

DANIEL K. ODELL

University of Miami Rosenstiel School of Marine and Atmospheric Science
4600 Rickenbacker Causeway
Miami, FL 33149

GROWTH CHARACTERISTICS OF YOUNG-OF-THE-YEAR WALLEYE, *STIZOSTEDION VITREUM VITREUM*, IN JOHN DAY RESERVOIR ON THE COLUMBIA RIVER, 1979

The walleye, *Stizostedion vitreum vitreum*, is becoming increasingly abundant in many of the large reservoirs of the Columbia River (Durbin[1]). Although the origin of this species in the Columbia River system is not entirely clear, Durbin (footnote 1) reported that walleye was introduced into the upper Clark Fork River, Idaho (a tributary of the Columbia River drainage), in the late 1940's (Figure 1). The large impoundments of the Columbia River, with turbid water conditions occurring through most of the spring and early summer, are providing walleye with suitable habitat. Scott and Crossman (1973) reported that walleye, throughout its range, reaches its greatest abundance in large turbid lakes and slow moving rivers.

[1]Durbin, K. 1977. News column. Oreg. Dep. Fish Wildl., Portland.

The increase in walleye population has generated considerable interest among sport fishermen throughout the Columbia River area (Harbour 1980). Because of its value as a game fish, some envision a significant new fishery similar to the historic fisheries of the Great Lakes region. Fisheries managers responsible for the survival of juvenile salmon, *Oncorhynchus* spp., and steelhead, *Salmo gairdneri*, are viewing the increase in walleye population with alarm, fearing that because of its highly piscivorous habits, it may become a significant salmonid predator.

Turbine intake gatewells at major dams in the Columbia River system are sampled each year to monitor the juvenile salmonid migrations (Raymond 1979). John Day Dam, a large hydroelectric project on the Columbia River, was completed in 1968 and created a reservoir (Lake Umatilla) 122 km long (Figure 1). Juvenile walleye was first observed in the gatewells at John Day Dam in 1973, and small numbers continued to be taken through 1978. In 1979, a large increase in the number of young-of-the-year walleye in the gatewells at John Day Dam was observed.

Information yielded by monitoring these young-of-the-year walleye in John Day Reservoir is presented in this paper. A comparison between growth of walleye in this reservoir and walleye populations from other areas is also given.

Methods

A large dip net, similar to that described by Bentley and Raymond (1968), was used to collect juvenile walleye from the turbine intake gatewells at John Day Dam. Young walleye were captured incidentally to the juvenile salmonid monitoring operation at the dam. A sample consisted of a 24-h composite catch removed daily from the gatewell via the dip net. Sampling extended from 1 March through 18 December 1979. All fish taken were measured for total length (TL) to the nearest millimeter and weighed to the nearest 0.1 g. Age was determined from scale samples taken in the manner described by Eschmeyer (1950). Scales were removed and examined from all specimens ≥100 mm TL to confirm that they were in fact young-of-the-year fish.

Results and Discussion

In 1979, the number of walleye entering the turbine intake gatewells at John Day Dam in-

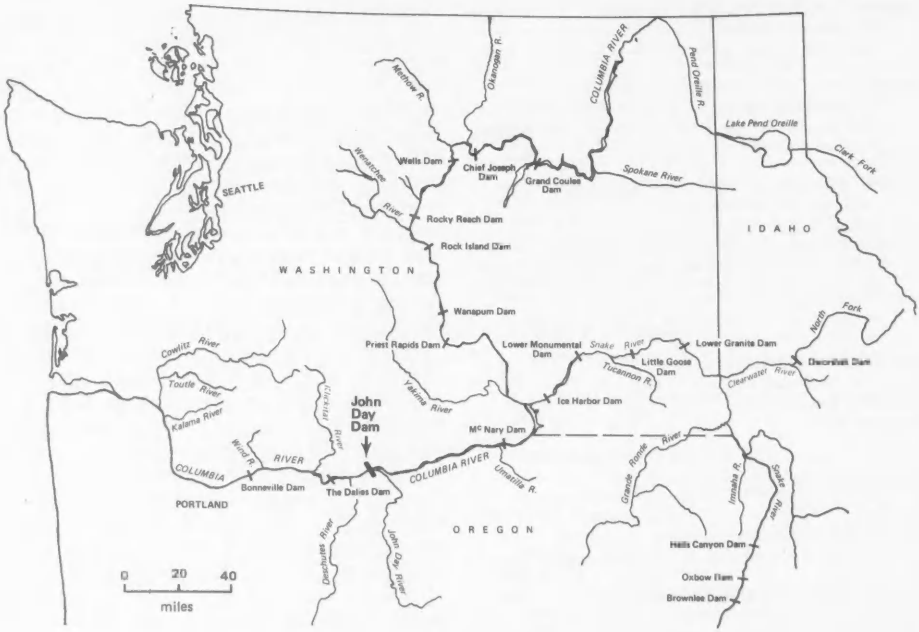

FIGURE 1.—Columbia River drainage.

creased significantly. From 1973 through 1978 fewer than 15 juvenile walleye were taken per year, whereas in 1979, several hundred were taken with similar fishing effort. Early in the season, an exact count was not possible because many of the small fish (<40 mm TL) fell through the mesh of the net [12.7 mm (½ in) stretched measure]. In 1979, young-of-the-year walleye was first taken in the gatewells in July and continued to be taken until sampling was suspended in mid-December.

Walleye normally spawns at water temperatures between 5.6° and 11.1° C (Scott and Crossman 1973). Hatching occurs in 21 d at water temperatures of 10°-12.8° C (Niemuth et al. 1972). Water temperatures at John Day Dam rose from 6.2° to 13.8° C during April and May 1979. At these temperatures one would expect hatching to extend through May, producing fry in the 40 mm class by early July.

Water temperatures in John Day Reservoir during the summer were near optimum for excellent growth of juvenile walleye. Huh et al. (1976) reported the growth of young-of-the-year walleye to be temperature dependent, with optimum growth occurring at 22° C. Water temperatures in John Day Reservoir fluctuated between 19° and 21° C for a 10-wk period extending from early July through September.

Total length of juvenile walleye increased an average of 11 mm/wk from July to October (Figure 2). This compares very favorably to the 13 mm/wk reported by Wolfert (1977) for walleye in Lake Erie. Mean length of young-of-the-year walleye in John Day Reservoir at the end of the 1979 growing season was 226 mm. Average weight by this time was 87.4 g (0.19 lb). Total length at the end of the growing season was only slightly less than reported for walleye in Lake Erie (Wolfert 1977) and considerably greater than lengths reported in Lake Gogebic, Mich. (Eschmeyer 1950); Red Lake, Minn. (Smith and Pycha 1960); and Oneida Lake, N.Y. (Forney 1966). Growth of young-of-the-year walleye in John Day Reservoir slowed steadily in November with declining water temperatures.

The presence of a larger number of walleye in the gatewell samples during 1979 indicates that the abundance of juvenile walleye appears to be increasing. The potential impact on salmonid

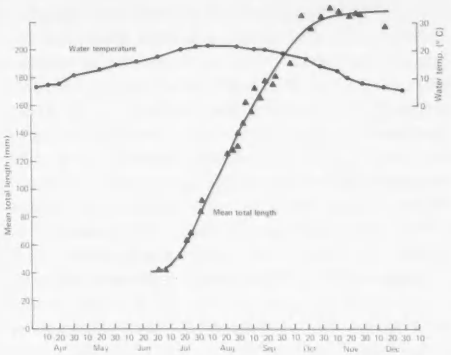

FIGURE 2.—First year growth of walleye and water temperature at John Day Dam on the Columbia river, 1979. Growth curve fitted by inspection (171 fish represented). Each point on the growth curve is the arithmetic mean of 3 to 12 specimens.

populations by the increasing abundance of walleye indicates a continuing need for monitoring walleye in this section of the Columbia River system.

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Literature Cited

BENTLEY, W. W., AND H. L. RAYMOND.
1968. Collection of juvenile salmonids from turbine intake gatewells of major dams in the Columbia River system. Trans. Am. Fish. Soc. 97:124-126.

ESCHMEYER, P. H.
1950. The life history of walleye, *Stizostedion vitreum vitreum* (Mitchill) in Michigan. Bull. Inst. Fish. Res., Mich. Dep. Conserv. 3, 99 p.

FORNEY, J. L.
1966. Factors affecting first-year growth of walleyes in Oneida Lake, New York. N.Y. Fish Game J. 13:146-167.

HARBOUR, D.
1980. Western walleye invasion. Sports Afield 183(3): 124-130.

HUH, H. T., H. E. CALBERT, AND D. A. STUIBER.
1976. Effect of temperature and light on growth of yellow perch and walleye using formulated food. Trans. Am. Fish. Soc. 105:254-258.

NIEMUTH, W., W. CHURCHILL, AND T. WIRTH.
1972. Walleye, its life history, ecology, and management. Wis. Dep. Nat. Resour. Publ. 227, 20 p.

RAYMOND, H. L.
1979. Effects of dams and impoundments on migrations of juvenile chinook salmon and steelhead from the Snake River, 1966 to 1975. Trans. Am. Fish. Soc. 108:505-529.

SCOTT, W. B., AND E. J. CROSSMAN.
1973. Freshwater fishes of Canada. Fish. Res. Board Can., Bull. 966 p.

SMITH, L. L., JR., AND R. L. PYCHA.
1960. First-year growth of the walleye, *Stizostedion vitreum vitreum* (Mitchill), and associated factors in the Red Lakes, Minnesota. Limnol. Oceanogr. 5:281-290.

WOLFERT, D. R.
1977. Age and growth of the walleye in Lake Erie, 1963-1968. Trans. Am. Fish. Soc. 106:569-577.

DEAN A. BREGE

Northwest and Alaska Fisheries Center Coastal Zone and Estuarine Studies Division
National Marine Fisheries Service, NOAA
2725 Montlake Boulevard East
Seattle, WA 98112

EFFECTS OF TEMPERATURE AND SALINITY ON EGG HATCHING AND LARVAL SURVIVAL OF RED DRUM, *SCIAENOPS OCELLATA*[1]

The red drum, *Sciaenops ocellata*, is a sciaenid fish distributed along the eastern coast of North America from Massachusetts to southern Florida and along the gulf coast at least as far south as Tampico, Mexico (Hildebrand and Schroeder 1928; Simmons and Breuer 1962). Spawning occurs in late summer through fall outside estuaries in nearshore coastal waters, and the young red drum is carried into the estuaries by tides and currents (Pearson 1929; Mansueti 1960). Late larvae and early juveniles have been collected in the shallow water of tidal flats and sea grass beds. The early planktonic stages, the eggs and yolk-sac larvae, have not been identified from field collections but have recently been described, based on specimens from laboratory-spawned red drum (Holt et al. 1981).

Temporal fluctuations in abundance of red drum result in annual variation in sport and commercial catches (Matlock and Weaver 1979). Variations in environmental factors such as temperature and salinity could affect egg incubation and larval survival, and ultimately year-class strength. Juveniles and adults are euryhaline and are found naturally in freshwater, in brackish

[1]University of Texas Marine Science Institute Contribution No. 466.

water estuaries, and most abundantly in salinities of 20-35‰ (Simmons and Breuer 1962). A wide temperature range of 2°-33° C can be tolerated as long as the temperature change is gradual (Gunter and Hildebrand 1951; Simmons and Breuer 1962). Little is known about the upper and lower limits of temperature and salinity and their effects on survival of eggs and early larval stages, or on early development and growth.

The objective of this study was to determine the optimum temperatures and salinities for hatching and growth of red drum eggs and larvae. Similar work on temperature and salinity effects on survival and development have been detailed for other marine species (Alderdice and Forrester 1971; Alderdice and Velsen 1971; May 1975).

Methods

Eggs were obtained from laboratory spawnings induced by manipulations of temperature and photoperiod to simulate natural seasonal changes (Arnold et al. 1977). Brood tank temperatures ranged from 24° to 26° C and salinities from 26 to 32‰. The most successful method for rearing larvae under our experimental conditions was the following: 1) Hatching at a density of 50-100 eggs in a 100 ml beaker with 10 ppm erythromycin; 2) feeding sequentially the dinoflagellate *Prorocentrum micans* (500/ml, day 2) and the rotifer *Brachionus plicatilis* (50-100/ml, day 3); 3) transferring larvae after 3-4 h feeding on rotifers to a Nitex[2] holding chamber in a 1 l beaker; 4) feeding *Artemia salina* nauplii to larvae (2/ml, beginning on day 7).

Water was changed every fourth day. The holding chambers were made from a cylinder of 300 μm Nitex net glued to a plastic Petri dish; the dish forming the bottom and the Nitex net the sides of the container. Air was introduced into the beaker outside the holding chamber to avoid producing turbulence and bubbles within the chamber. Test salinities were made with filtered seawater (1 μm) diluted with deionized water or concentrated with artificial sea salts (Instant Ocean). Temperatures were maintained within 0.5° C and illumination from fluorescent room lamps was continuous. Percentage hatch, percentage survival of the larvae to 24 h and 14 d, and standard length (millimeters) of 14-d-old larvae were measured to determine the influence of temperature and salinity. Analyses were conducted on the arc sine transformation of the percentages. Two-way factorial analysis of variance was used to test for significant differences among eggs and larvae reared at 12 salinity-temperature conditions.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Results

Results of initial tests of the influence of different temperature-salinity combinations on hatching and survial of red drum showed poor hatching rates at low salinity (10‰) over all temperatures except 25° C. Red drum eggs floated in 25‰ or greater salinity and sank to the bottom in lower salinities. High temperatures (30° and 35° C) and high salinities were associated with poor survival of the yolk-sac larvae. Based on these results four salinities (15, 20, 25, and 30‰) and three temperatures (20°, 25°, and 30° C) were used to determine conditions for optimum survival and growth of red drum eggs and larvae. The ranges of salinity and temperature selected are representative of conditions occurring in coastal waters during the normal spawning period.

TABLE 1.—Percentage hatch and larval survival of red drum for each salinity-temperature condition tested. Initially each replicate contained 50-100 eggs.

Salinity (‰)	Temp (° C)	Hatch (%) Replicates									Mean	24-h-old larvae (%) Replicates					Mean
15	20	100	95	91	79	94	100	100	97	96	95	93	100	100	97	98	97
	25	87	58	3	10	84	80	100	100	65	87	28	98	95	94	93	83
	30	89	50	72	64	61	79	100	100	77	89	22	84	98	1	1	49
20	20	100	96	94	85	98	92	100	100	96	97	96	100	100	98	97	98
	25	86	98	34	74	92	88	100	100	84	86	98	100	100	100	99	97
	30	90	71	94	72	57	56	100	100	80	90	55	86	83	25	83	70
25	20	100	98	84	87	96	98	100	100	95	97	96	100	100	98	97	98
	25	100	98	95	89	98	97	100	100	97	100	98	100	100	99	100	100
	30	96	100	96	80	96	100	100	100	96	79	72	98	100	94	95	90
30	20	100	98	91	94	94	100	100	100	97	98	98	100	100	100	98	99
	25	100	100	100	100	98	98	100	100	100	100	98	100	100	100	100	100
	30	100	100	91	100	98	100	100	100	99	82	79	100	100	96	98	93

The best conditions for hatching and 24-h larval survival were 30‰ salinity and 25° C (Table 1). Analysis of variance of the hatching data showed temperature (T) and the temperature-salinity interaction ($T \times S$) effects to be of borderline significance ($0.10 > P > 0.05$); only salinity was significant ($P < 0.05$) (Table 2). A pattern of decrease in percent hatch with increase in temperature at the lower salinities (15 and 20‰), but not at the higher salinities (Table 1), is indicative of the $T \times S$ interaction. Hatching was significantly greater at the two higher salinities than at lower salinities (Table 3).

Survival of larval red drum to 24 h was influenced by both temperature and salinity. Poorest survival was at 30° C and 15‰ (Table 3).

Temperature was associated with significant differences in survival of 2-wk-old larvae (Table 2). The lowest temperature (20° C) resulted in reduced survival rate. The effect of temperature on larval growth rate was pronounced; growth at 20° C was much slower than at 25° or 30° C (Table 4). Salinity had little influence on growth.

TABLE 3.—Mean percentage hatch, 24-h survival, and 2-wk survival of red drum over all conditions. Individual means were compared using Duncan's multiple range test. Any two means connected by the same line were not significantly different ($P < 0.05$).

Item	15‰	20‰	25‰	30‰	20° C	25° C	30° C
% hatch	76.46	86.54	96.17	98.42	96.09	86.47	87.87
% 24-h survival	64.57	75.19	81.79	84.20	98.04	94.71	75.42
% 2-wk survival	6.00	4.17	5.42	4.92	0.37	8.00	7.00

TABLE 4.—Standard length (millimeters) of red drum larvae that survived 2 wk.

Salinity (‰)	20° C			25° C			30° C		
	Mean	SD	n	Mean	SD	n	Mean	SD	n
15	2.80		1	4.90	1.137	18	6.20	1.316	38
20	3.35	0.212	2	4.60	1.046	34	5.80	1.500	17
25	3.20		1	4.70	1.078	27	7.00	1.794	29
30	3.55	.071	2	4.75	.937	30	6.80	2.019	13

Discussion

Salinity was important for hatching and 24-h survival but not for 2-wk survival. Red drum eggs developed successfully to feeding larvae at salinities of 10-40‰ at 25° C; at other temperatures the salinity range for 75% hatch was reduced to 15-30‰. In low salinities, eggs sank to the bottom; as Fonds (1979) explained for the common sole, *Solea solea*, crowding and possible respiratory stress contributed to reduced survival under these conditions. In natural populations high mortality of eggs developing on the bottom would be expected.

Red drum eggs may have been acclimated to the higher salinities since salinities for best hatching were very near the salinities of the maturation and spawning tanks (26-30‰). Solemdal (1967) reported that the osmotic concentration of the ovarian fluid affected the buoyancy of flounder eggs and that both could be changed experimentally. Kinne and Kinne (1962) found that the salinity of the water in which the parents lived affected the response of developing cyprinodont fish to salinity. Differences in response were explained as being primarily nongenetic adaptations to the spawning salinity (Kinne 1962). Conversely, May (1975) found salinity tolerance of *Bairdiella icistia* eggs was not affected by acclimation of the parent fish to low salinity and suggested that salinity responses determined for eggs accurately predict reaction to different salinities in nature.

Temperature became increasingly important as the larvae developed. Apparently contradictory results showed low temperature (20° C) to be superior for 24-h survival, but inferior for 2-wk survival and growth. With low temperature, development and probably metabolism were slowed to the extent that growth and even mortality were delayed. The time spent in the yolk-sac stage is temperature dependent; ranging from 40 h at 30° C to 85 h at 20° C (Holt et al. 1981). Blaxter (1969) cautioned that high yolk-sac utilization efficiency may result from low activity which becomes a liability when it is reflected in

TABLE 2.—Analysis of variance of percent hatch and survival of red drum eggs and larvae subjected to various temperature-salinity conditions.

	% hatch				24-h-old larvae				2-wk-old larvae			
Source	df	MS	F	P	df	MS	F	P	df	MS	F	P
Temperature (T)	2	459.94	2.44	0.09	2	3,090.70	16.43	0.00	2	450.69	20.66	0.00
Salinity (S)	3	1,634.80	8.67	0	3	1,386.77	7.37	0	3	4.56	.21	.89
$T \times S$	6	400.18	2.12	.06	6	352.40	1.87	.10	6	6.54	.30	.92
Error	84	188.41			60	188.12			12	21.82		

low feeding activity. This was clearly the case with the few fish that survived 2 wk in 20° C. These larvae were inactive, were not seen catching prey, and they grew very slowly. Larvae raised at higher temperatures actively attacked and ate prey as soon as it was introduced to the chamber.

Based on these results we hypothesize that red drum spawning success and subsequent year-class strength will be adversely affected by the early onset of low water temperatures. Red drum is a fall spawner and the young must survive and grow at the winter temperatures found in low-temperate estuaries; bay water temperatures often fall below 20° C in November and average 15°-17° C in December in Texas (Martinez 1975). The results indicate that for the first week or so the larvae are stenothermal. The ability to find and catch prey when the yolk sac has been absorbed is a critical phase in larval survival (May 1974). Once temperature in the coastal water declines to 20° C red drum larvae that have reached the critical phase may not be able to find and catch prey. An early reduction in nearshore water temperatures could result in an unsuccessful red drum reproductive effort for that year. Indirect evidence implicates the importance of temperature to reproductive success in that our laboratory-reared red drum stop spawning when the temperature drops below 20° C. This phenomenon may account for the earlier spawning of red drum in its more northerly range (Mansueti 1960) and prolonged spawning in warmer regions (Jannke[3]).

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Literature Cited

ALDERDICE, D. F. AND C. R. FORRESTER.
1971. Effects of salinity and temperature on embryonic development of the petrale sole (*Eopsetta jordani*). J. Fish. Res. Board Can. 28:727-744.

ALDERDICE, D. F., AND F. P. J. VELSEN.
1971. Some effects of salinity and temperature on early development of Pacific herring (*Clupea pallasi*). J. Fish. Res. Board Can. 28:1545-1562.

ARNOLD, C. R., W. H. BAILEY, T. D. WILLIAMS, A. JOHNSON, AND J. L. LASSWELL.
1977. Laboratory spawning and larval rearing of red drum and southern flounder. Proc. Annu. Conf. Southeast Assoc. Fish Wildl. Agencies 31:437-440.

BLAXTER, J. H. S.
1969. Development: eggs and larvae. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. III, p. 177-252. Acad. Press, N.Y.

FONDS, M.
1979. Laboratory observations on the influence of temperature and salinity on development of the eggs and growth of the larvae of *Solea solea* (Pisces). Mar. Ecol. Prog. Ser. 1:91-99.

GUNTER, G., AND H. H. HILDEBRAND.
1951. Destruction of fishes and other organisms on the south Texas coast by the cold wave of January 28-February 3, 1951. Ecology 32:731-736.

HILDEBRAND, S. F., AND W. C. SCHROEDER.
1928. Fishes of Chesapeake Bay. Bull. U.S. Bur. Fish. 43(1), 366 p.

HOLT, J., A. G. JOHNSON, C. R. ARNOLD, W. A. FABLE, JR., AND T. D. WILLIAMS.
1981. Description of eggs and larvae of laboratory reared red drum *Sciaenops ocellata*. Copeia 1981:751-756.

KINNE, O.
1962. Irreversible nongenetic adaptation. Comp. Biochem. Physiol. 5:265-282.

KINNE, O., AND E. M. KINNE.
1962. Rates of development in embryos of a cyprinodont fish exposed to different temperature-salinity-oxygen conditions.. Can. J. Zool. 40:231-253.

MANSUETI, R. J.
1960. Restriction of very young red drum *Sciaenops ocellata*, to shallow estuarine waters of Chesapeake Bay during late autumn. Chesapeake Sci. 1:207-210.

MARTINEZ, A. R.
1975. Coastal hydrological and meteorological study. Tex. Parks Wildl. Dep. Coastal Fish. Branch Rep. 1975:100-157.

MATLOCK, G. C., AND J. E. WEAVER.
1979. Assessment and monitoring of Texas coastal finfish resources. Tex. Parks Wildl. Dep. Coastal Fish. Branch Rep., 247 p.

MAY, R. C.
1974. Larval mortality in marine fishes and the critical period concept. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 3-19. Springer-Verlag, N.Y.
1975. Effects of temperature and salinity on fertilization, embryonic development, and hatching in *Bairdiella icistia* (Pisces: Sciaenidae), and the effect of parental salinity acclimation on embryonic and larval salinity tolerance. Fish. Bull., U.S. 73:1-22.

PEARSON, J. C.
1929. Natural history and conservation of redfish and other commercial sciaenids on the Texas coast. Bull. U.S. Bur. Fish. 44:129-214.

SIMMONS, E. G., AND J. P. BREUER.
1962. A study of redfish, *Sciaenops ocellata* Linn., and the

[3]Jannke, T. E. 1971. Abundance of young sciaenid fishes in Everglades National Park, Florida, in relation to season and other variables. Univ. Miami Sea Grant Tech. Bull. 11, 28 p.

black drum, *Pogonias cromis* Linn. Publ. Inst. Mar. Sci. Univ. Tex. 8:184-211.

SOLEMDAL, P.

1967. The effect of salinity on buoyancy, size and development of flounder eggs.. Sarsia 29:431-442.

JOAN HOLT
ROBERT GODBOUT
C. R. ARNOLD

University of Texas Marine Science Institute
Port Aransas Marine Laboratory
Port Aransas, TX 78373

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